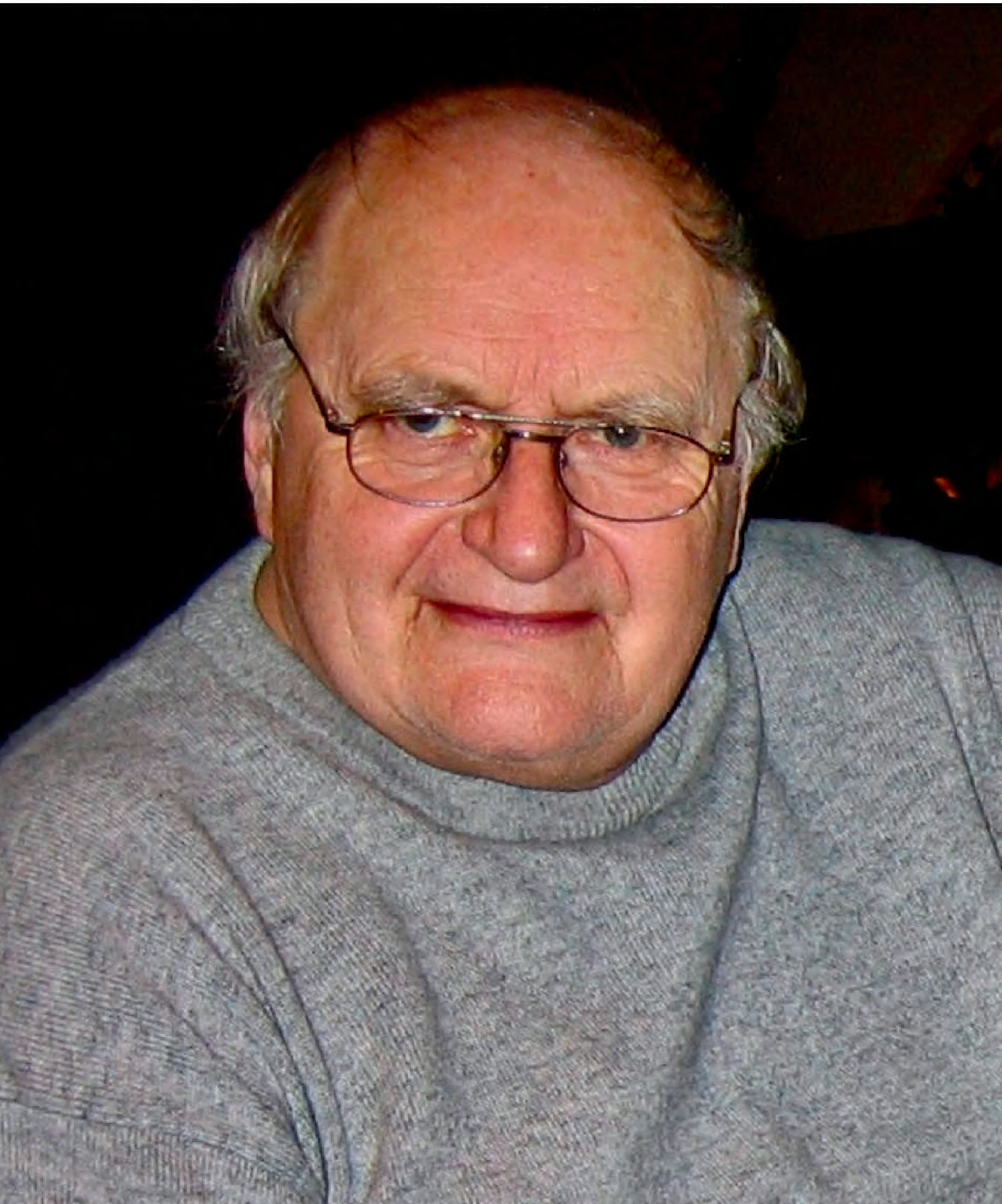
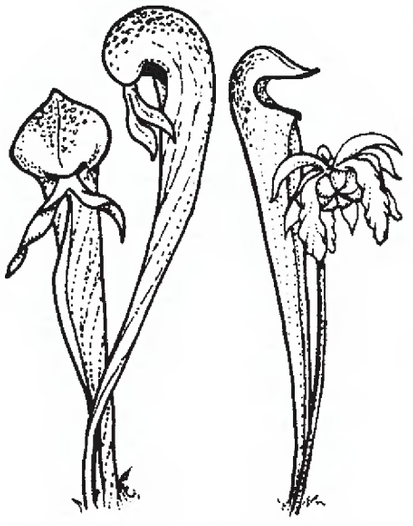
CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society

Volume 50, No. 4 December 2021





CARNIVOROUS PLANT NEWSLETTER

Journal of the International Carnivorous Plant Society
www.carnivorousplants.org

Volume 50, Number 4
December 2021

Front Cover: Siegfried Jost Casper at his workplace, the Institut für Spezielle Botanik in Jena, Germany, on 2 January 2004. Photo provided by Hermann Manitz. The photographer is Rosmarie Stimper. Article on page 165.

Back Cover: *Pinguicula casperi*, named in honor of the late Prof. S. Jost Casper, flowering at its natural habitat in Durango state, Mexico. Photo by David Juárez. Article on page 165.

Carnivorous Plant Newsletter is dedicated to spreading knowledge and news related to carnivorous plants. Reader contributions are essential for this mission to be successful. Do not hesitate to contact the editors with information about your plants, conservation projects, field trips, or noteworthy events. Advertisers should contact the editors. Views expressed in this publication are those of the authors, not the editorial staff.

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Date of effective publication of the September 2021 issue of Carnivorous Plant Newsletter: August 6, 2021.

The ICPS is the International Cultivar Registration Authority (ICRA) for the names of cultivated carnivorous plants according to the International Code of Nomenclature for Cultivated Plants. Send relevant correspondence to the ICPS, Inc.

Carnivorous Plant Newsletter is published quarterly in March, June, September, and December by the ICPS, Inc., 2121 N. California Blvd., Suite 290, Walnut Creek, CA 94596, USA. Periodicals postage paid at Walnut Creek, CA and additional mailing offices. Postmaster: Send address changes to ICPS, Inc., 2121 N. California Blvd., Suite 290, Walnut Creek, CA 94596, USA. Printed by Allen Press, Inc., 810 E. 10th Street, Lawrence, KS 66044. Logo and masthead art: Paul Milauskas.
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2021 ICPS Lifetime Achievement Award
Professor Dr. Siegfried Jost Casper

It is with mixed emotions that on behalf of the ICPS, I announce that the recipient of the 2021 ICPS Lifetime Achievement Award, is Jost Casper. We are delighted to present this award but saddened by the recent passing of Jost before he was able to receive the award itself. The Lifetime Achievement Award is presented in recognition of an individual's outstanding leadership and contribution to the field of Carnivorous Plants. This may be achieved in research, cultivation, conservation, or other ways deemed to be above and beyond the everyday with a significant impact on the field.

Professor Dr. Siegfried Jost Casper is the recipient of the 2021 ICPS Lifetime Achievement Award, for his significant impact on the understanding of the genus *Pinguicula* and his continuous scientific contributions in this field, which led to numerous publications on *Pinguicula*, including several new species described by him, an elaborate monograph, as well as several taxonomic, morphological, and cytological treatments of the genus.

As recipient of this award, Jost's estate will be presented with an original botanical artwork by François Sockhom Mey commissioned by the ICPS specifically for this occasion and permanent recognition on the ICPS website. The award was given to Jost Casper posthumously, and was handed out to Dr. Hermann Manitz, who is responsible for Jost Casper's scientific legacy at Jena Herbarium and the University of Jena, Germany.

Richard Nunn
President ICPS

The Award Painting by François Sockhom Mey, showing *Pinguicula grandiflora* subsp. *rosea*, one of the first taxa named by Jost Casper, at Casper's former workplace in the herbarium of the University of Jena, Germany. Photo taken by Jörn Hentschel and Hermann Manitz.

Siegfried Jost Casper (1929–2021)

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Siegfried Jost Casper was born on January 12th, 1929 in Oberneuschönberg (united with Olbernhau, Saxony, from 1950) as the son of the teacher Siegfried Casper and his wife Helene Casper (née Zimmermann).

From 1935 to 1947 Casper attended schools in Oberneuschönberg, Leipzig, and Zschopau. From 1948 to 1951 he worked as a teacher at a primary school in Leipzig. This was followed by a degree in biology at the Universities of Leipzig and Jena, which he completed in 1956 with a thesis on the embryology of the genus *Cyclamen* at the Institute for Special Botany under Otto Schwarz (1900–1983). From 1956 to 1961 he was a scientific assistant at the Institute for Special Botany at the Friedrich Schiller University in Jena. In December 1960 he received his Dr. rer. nat. in Jena with the thesis "Revision of the genus *Pinguicula* in Eurasia".

Figure 1: Jost Casper and his wife Rosmarie, after whom he named *Pinguicula rosmarieae* in 2020, on a common excursion in 2004 to a local gypsicolous population of *Pinguicula vulgaris* ("*P. gypsophila*") in Thuringia, Germany. Photo by Rosemarie Stimper.

Jost Casper was also interested in "lower" organisms (protists) early on, also motivated by the work of Johanna Rosmarie Focke (1933–2020) from the department of Protophyta Science of the Institute for Special Botany, who became his wife. His first lecture in Jena (Special Botany III, 1961) dealt with these groups. From 1962 to 1965, Casper was senior scientific assistant at the Research Center for Limnology of the Academy of Sciences (AdW) in Jena; later as deputy director and from 1969 to 1989 as head of this academic facility. During this time, he completed his habilitation thesis (qualification for professorship) in 1965 at the Friedrich Schiller University in Jena with the Monograph of the genus *Pinguicula* L. (Casper 1966).

Further extensive publications of this time covered basic features of a natural system of microorganisms (Casper 1974), the processing of the "Peridophyta and Anthophyta" together with Heinz-Dieter Krausch (1928–2020) for the 2nd edition of the "Freshwater flora of Central Europe" (1980 to 1981) and a publication on Lake Stechlin (Casper 1985). He was also the editor of "Limnologica" and "Archiv für Protistenkunde" (continued as "Protist" since 1998). From October 1, 1992 to September 30, 1996, S. J. Casper was Director of the Institute for Special Botany at Friedrich Schiller

University Jena as the successor to Gerhard Franz Klotz (1928–2017). In September 2007 he and his wife moved to Dresden for family reasons. Most recently he lived there in a retirement home. Here he died on June 13th, 2021. His scientific legacy was donated to the Herbarium Haussknecht (JE) of the Friedrich Schiller University Jena.

Figure 2: Jost Casper at his last workplace in a retirement home in Dresden, where he continued his studies on *Pinguicula*, and wrote – among other publications – his monograph on the Caribbean butterworts (Casper 2019). Photo taken by Max von Tilzer on the occasion of Casper's 90th birthday.

Jost Casper and the genus *Pinguicula*

Jost Casper was passionate about *Pinguicula*. In his works written in German, he almost never used the common German vernacular name ("Fettkraut") but instead adopted to the German language the genus' scientific name, speaking a bit oddly about "die Pinguikeln" (that would translate into "the penguicles"). He also loved to "Germanize" other technical terms from foreign languages. For the multi-author works "*Pinguicula* of Latin America" (Lampard *et al.* 2016) and "*Pinguicula* of the Temperate North" (Roccia *et al.* 2016) in personal correspondence with the authors he impishly referred to them as the "Vielmännerbuch" ("many-men-book" or "polyandrous book") in analogy to the "Viermännerbuch" ("four-men-book") which is German jargon for Strasburger's textbook of Botany (Kadereit *et al.* 2014) that is traditionally written by four main authors covering the main branches of Botany. His scientific articles are filled with a tremendous amount of information, and he often seemed to have problems fitting all of his knowledge into the main text body. Therefore, Jost Casper commonly used footnotes to accommodate additional information on collectors, etymology, geography, or other interesting facts.

Jost Casper dedicated his scientific work to the research on Lentibulariaceae taxonomy, systematics and biology, especially of the genus *Pinguicula*, which he studied more intensively than anyone else before him and until today. His impact on that field is unreached, spanning 61 years of academic work and scientific research on Lentibulariaceae, cumulating in more than 30 major scientific publications on *Pinguicula*, including his benchmark monograph on the genus (Casper 1966), a recent monograph on the Caribbean *Pinguicula* species (Casper 2019), as well as numerous significant works on the systematics, morphology, chorology, and chromosome numbers of *Pinguicula*, but also some on *Utricularia*, as well as other floristic treatments, including carnivorous plant genus treatments for local floras (see appended Publication List). Even being in his 90s, Jost Casper continued his research and prolific publication efforts on *Pinguicula*, resulting in at least one major publication on the genus every 2-3 years. Casper named 23 species of *Pinguicula*, 2 subspecies, and he additionally coined names for several sections, subsections, series, and other infrageneric groups of *Pinguicula*. Not all of his new names were validly published; Casper casually referred to these names as his "illegitimate children" (J. Casper, pers. comms.). He studied *Pinguicula* from all over the genus' range (with its diversity centers in Europe, Mexico, and the Neotropics), reshaped the

infrageneric classification of the genus and also made profound contributions to the karyology and phylogeny of the genus. His unbroken effort and in particular his scientific achievements (that vastly exceed his work to promote our understanding of the genus *Pinguicula*) are indisputable and fully deserve our admiration and appreciation. Even more so, as his thorough morphological studies on *Pinguicula* are largely based on careful examination of herbarium material, which he received from colleagues all over the world. Unfortunately, restricted in the former German Democratic Republic (GDR), he was not allowed to travel himself to the destinations where the plants he admired so much are growing. Jost Casper (pers. comms. to AF, 2017) explained that he had difficulties accessing herbarium material from some countries during the work on his *Pinguicula* monograph in the 1960s. For example, he was not able to consult one of the World's largest herbarium collections of Lentibulariaceae at Kew Herbarium, England, because he was not allowed any correspondence with Great Britain at that time. He referred to that as the "KEW-gap" of his monograph and explained it to be caused by the "preposterous situation during the Stalinism era" (J. Casper, pers. comm. 2017).

Together with the late Peter Taylor (1926–2011), the carnivorous plant community is now missing the leading taxonomic experts and monographers of Lentibulariaceae. We hope that their spirits meet up on the other side, whence they might appraise their posterity's modest taxonomic efforts with mildness.

Jost Casper as a lecturer and teacher

Jan Schlauer had the pleasure (in 1999) to witness him as a lecturer (on the genus *Dracaena*, see Casper 2000), and the term "impressive" is too weak to describe this experience on him. Already back then Casper was an emeritus. Even though the presentation was "old school" in the best of any meanings, it was educative in every aspect. It was a diapositive slide presentation and the person who operated the projector was clumsy enough to drop the slides in an unsuccessful effort to change trays in the middle of Casper's lecture. The second half of the presentation used randomly reassembled slides with upside-down or otherwise disoriented pictures. This introduced new unexpected spins and twists to the original story. Still Casper managed to make perfect sense of his unintended surprise show. Without a manuscript he told the modified story as if it followed the original plot in a perfect diction without stops or delays (which can be a challenge even when you are reading the text from a teleprompter). From that date Jan knew what a real "Professor" should be like and that he could never hope to reach Casper's level of mastery.

Figure 3: Two *Pinguicula* species have been named in honour of Jost Casper: *Pinguicula casperi* from Mexico (left; see also back cover) and *P. casperiana* from Spain (right; see also article by A. Roccia on p. 198). Photo of *P. casperi* by David Juárez, photo of *P. casperiana* by Oliver Gluch.

Jost Casper's nomenclatural legacy

Eponymy – plants named in honor of Jost Casper:

Pinguicula casperi H.D.Juárez & Zamudio (2018)
Pinguicula casperiana M.B.Crespo, Mart.-Azorín, M.Á.Alonso & L.Sáez (2020)

Taxa named by Jost Casper (vascular plants only)

Pinguicula agnata Casper (1963: 14)
Pinguicula apuana Casper & Ansaldi (2009: 13)
Pinguicula baezensis Casper (2019: 23)
Pinguicula balcanica Casper (1962: 105)
Pinguicula balcanica subsp. *pontica* Casper (1970: 285)
Pinguicula bissei Casper (2004: 2)
Pinguicula caryophyllacea Casper (2004: 8)
Pinguicula cubensis Urquiola & Casper (2003: 170)
Pinguicula cyclosecta Casper (1963: 11)
Pinguicula grandiflora subsp. *rosea* (Mutel) Casper (1962: 85)
Pinguicula imitatrix Casper (1963: 12)
Pinguicula infundibuliformis Casper (2003: 144)
Pinguicula jaraguana Casper (2003: 141)
Pinguicula kondoi Casper (1974: 1)
Pinguicula lippoldii Casper (2007: 77)
Pinguicula longifolia subsp. *caussensis* Casper (1966: 154) = *Pinguicula caussensis* (Casper) Roccia (2016: 127)
Pinguicula longifolia subsp. *reichenbachiana* (Schindler) Casper (1962: 71)
Pinguicula mariae Casper (2009: 3)
Pinguicula moaensis Casper (2019: 93)
Pinguicula nevadensis (H.Lindb.) Casper (1962: 112)
Pinguicula orthoceras Casper (2019: 97)
Pinguicula poldinii J.Steiger & Casper (2001: 28)
Pinguicula rosmarieae Casper, Bussmann & T.Henning (2020: 111)
Pinguicula sharpii Casper & K.Kondo (1977: 112)
Pinguicula toldensis Casper (2007: 85)
Pinguicula sect. *Agnata* Casper (1963: 331)
Pinguicula sect. *Ampullipalatum* Casper (1963: 334)
Pinguicula sect. *Cardiophyllum* Casper (1962: 34)
Pinguicula sect. *Discoradix* Casper (1963: 332)
Pinguicula sect. *Heterophyllum* Casper (1963: 332)

Pinguicula sect. *Homophyllum* Casper (1963: 325)
Pinguicula sect. *Isoloba* Casper (1963: 330)
Pinguicula sect. *Longifoliae* (Casper) Blanca, Ruíz Rejón & Reg.Zamora, as '*Longifolia*' (1999: 347)
Pinguicula sect. *Micranthus* Casper (1962: 45)
Pinguicula sect. *Nana* Casper (1962: 41)
Pinguicula subsect. *Agnata* Casper (1966: 92)
Pinguicula subsect. *Agnatiformis* Casper (1966: 75)
Pinguicula subsect. *Alpiniformis* Casper (1966: 114)
Pinguicula subsect. *Caudatopsis* Casper (1966: 144)
Pinguicula subsect. *Heterophylliformis* Casper (1966: 113) = *Pinguicula* sect. *Heterophylliformis* (Casper) A.Fleischm. & Roccia (2018: 76)
Pinguicula subsect. *Homophylliformis* Casper (1966: 96)
Pinguicula subsect. *Isolobopsis* Casper (1966: 99)
Pinguicula subsect. *Orcheosanthopsis* Casper (1966: 103)
Pinguicula subsect. *Orchidopsis* Casper (1966: 136)
Pinguicula subsect. *Primuliformis* Casper (1966: 80)
Pinguicula subsect. *Pumiliformis* Casper (1966: 71) = *Pinguicula* sect. *Pumiliformis* (Casper) Roccia & A.Fleischm. (2018: 75)
Pinguicula subsect. *Violiformis* Casper (1966: 133)
Pinguicula ser. *Agnatae* Casper (1963: 332)
Pinguicula ser. *Albidae* Casper (1963: 332)
Pinguicula ser. *Alpinae* Casper (1963: 335)
Pinguicula ser. *Andinae* Casper (1963: 334)
Pinguicula ser. *Antarcticae* Casper (1963: 334)
Pinguicula ser. *Balcanicae* Casper (1962: 105)
Pinguicula ser. *Caudatae* Casper (1966: 139)
Pinguicula ser. *Cyclosectae* Casper (1966: 136)
Pinguicula ser. *Grandiflorae* Casper (1962: 74)
Pinguicula ser. *Hispanicae* Casper (1962: 112)
Pinguicula ser. *Longifoliae* Casper (1962: 61)
Pinguicula ser. *Montanae* Casper (1962: 88)
Pinguicula ser. *Prealpicae* Casper (2009: 13)
Pinguicula ser. *Pumilioidae* Casper (1966: 80)
Pinguicula ser. *Septentrionales* Casper (1962: 114)
Pinguicula ser. *Variegatae* Casper (1963: 335)

Non-carnivorous taxa

Najas marina subsp. *intermedia* (Wolfgang ex Gorski) Casper (1979)

Publication List of S. Jost Casper (chronological, only covering CP-related publications)

Casper, S.J. 1959. Über *Pinguicula reichenbachiana* Schindler in Italien. Feddes Repert. 61: 274-280.

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My first experience with the genus *Pinguicula* and the manuscripts of Jost Casper

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It must have been the early eighties of the last century when I started with carnivorous plants. In those days plants like *Pinguicula* were hard to get and I had to drive to Hameln, in Germany, where a small nursery owned by Harald Weiner could provide me with several *Drosera*, *Utricularia*, and Mexican *Pinguicula* species. He had an enormous list of plants he grew and more than once I argued about the fact that when my *Pinguicula*'s flowered, many of them turned out to be *P. moranensis* or very similar to that. Later I ordered plants from him by mail (post), but the books I had then (Slack and Kondo) only showed a few good photos of *Pinguicula* flowers being well named. It took me several years before I really got into *Pinguicula*… it turned out to be a fever!

In 1987 I was given the opportunity to buy a copy of Casper's 'Monograph of Pinguicula' (1966), that in the following years had become a kind of bible to me. I'd studied the pile of paper almost day and night, first of all to get behind the mis-labelling of my plants, and in order to study the taxonomy of the whole genus with the Mexican species in particular. Through reverential notes and sources I started to collect Casper's older publications as well as those of other authors (DeCandolle, Humboldt, Bonpland, Kunth, Ernst), and after that the more modern authors. I'd spend many hours copying from books and journals in university libraries in order to collect as many articles and publications as possible. Madness(?)… no(!)… pure interest. Next to *Drosera*, *Utricularia*, and others, I found *Pinguicula* more my study subject.

Although Casper's intensive monograph was based on herbarium specimens, it provided me with more than enough information about every subject of a single plant. After a speed-course in Latin, I was able to understand the technical writing which was valuable in getting the whole picture. When I understood the structure of several keystones within the genus (subgenus, section, subsection, etc.), I was waiting for a possibility to describe a new species myself.

In 1989 I organized a 4-week fieldtrip to Mexico in order to study and photograph the plants in their natural habitat. I brought notes on habitat places from Casper's monograph with me, but many of them were very old, some of them up to 150 years. I remember our first finding when struggling and wandering around Real del Monte in the state of Hidalgo. We were looking for *P. macrophylla* and the description said 'El Chico', in the shade of the mountain. To cut a long story, we crossed a running stream and while walking along a narrow trail on a northern slope one of us found a flower on a short stem, but there was no plant just a little hole. *Utricularia*? No, the flower was too large for that so we dug and found a winter-rosette, something I had never seen before. *P. macrophylla*? It was only until the next day that we knew we had found *P. acuminata*. Rediscovered after 150 years, although from a non-Mexican perspective. Still… that first trip we found 6 species thanks to Casper's monograph, but even more so the knowledge of how and where *Pinguicula* is growing and why. It's all there.

A few days ago, I got the sad news from Jan Schlauer that Casper had died in June this year. We shall miss him as a person whose affection and interest on the subject was more than just being an author… he was my teacher.

On the occasion of the death of Prof. Dr. phil. Siegfried Jost Casper (1929–2021)

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In 1965 I wrote my Matura thesis on *Pinguicula* and in the following years obtained practically all publications on this genus. As the culmination of my search for literature, I found the *Pinguicula* monograph by Siegfried Jost Casper, which appeared in 1966 but was soon out of print, at a Berlin science antiquarian bookstore. Through the publishing house I was able to find the address of the author whom I first contacted by letter in September 1969. Telephone contact or a visit to Jena, where Casper lived, was impossible in view of the political situation in the former GDR. Since then, around 100 letters and later 312 e-mails to and from Casper have accumulated. The *Pinguicula* monograph was actually his so-called habilitation thesis with regard to an appointment as professor at the Friedrich Schiller University in Jena. I only found out why that failed after the fall of the Berlin Wall (1989) on the occasion of Casper's visit to Bern (which was later followed by several mutual visits): Because of the spying by the GDR Stasi, written reports about private life would have been too dangerous. Disgusted by the Ulbricht politics of the GDR, Casper and his family made meticulous preparations in 1962 for an escape to the West. On the evening before the escape, he informed the only person, his best friend of many years, a professor at the University of Jena, why he would no longer appear at the institute the next morning. This supposedly most trustworthy 'friend' advised the Stasi that same night: The cleverly prepared escape failed and Casper lost his tenure, his job, and the expected habilitation. Casper's wife had to testify against him in order to keep her part-time job as a hydrologist. For 30 years under most miserable financial conditions, Casper reactivated his profound knowledge of music and wrote several publications on works by Johann Sebastian Bach, which our musicology professor of the University of Bern classified as "absolutely professional". Thanks to the good trade relations between the GDR and Cuba (sugar agreement), Casper, although not allowed to travel, was able to participate in joint investigations of the *Pinguicula* taxa of Cuba, during which he described seven new species formally despite adverse conditions. In the description of the species, apart from the meticulous morphological and distribution details, I was particularly impressed by his excellent knowledge of Latin. In addition to his mother tongue German, Casper spoke and wrote English, Russian, French, and had a basic knowledge of Italian. In 1992, Casper was finally rehabilitated by the rector of the University of Jena, so that at the age of almost 64 he could fully resume his scientific work on the taxonomy, systematics and genetics of the genus *Pinguicula*. As professor and director of the Botanical Garden at the Institute for Special Botany at the University of Jena, he was actively supported by Prof. Mark Hellwig and Ms. Rosemarie Stimper, with whom he made numerous chromosome counts and performed DNA sequencing. The scientific achievements of Jost Casper are enormous: In addition to the 223-page *Pinguicula* monograph (1966), he published the 2 volumes on Tracheophytes for 'Freshwater flora of Central Europe' in 1980-81 as a joint work with Prof. H.-D. Krausch, the chapters on algae in 'Urania Pflanzenreich' (1991), and a series of publications on various botanical topics, plus 25 original descriptions/new combinations of *Pinguicula* species and subspecies! These are *P. agnata*, *P. apuana*, *P. baezensis*, *P. balcanica*, *P. balcanica* subsp. *pontica*, *P. bissei*, *P. cayophyllacea*, *P. cubensis* (with Urquiola), *P. cyclosecta*, *P. grandiflora* subsp. *rosea* (Mutel), *P. imitatrix*, *P. infundibuliformis*, *P. jaraguana*, *P. kondoi*, *P. lippoldii*, *P. longifolia* subsp. *caussensis*, *P. longifolia* subsp. *reichenbachiana* (Schindler), *P. mariae*, *P. moaensis*, *P. nevadensis* (H.Lindb.), *P. orthoceras*, *P. poldinii* (with Steiger), *P. rosmarieae*, *P. sharpii* (with Kondo), and *P. toldensis*. *Pinguicula casperi* H.D.Suarez & Zamudio (2018) from Mexico and *P. casperiana* M.B.Crespo *et al.* (2020) from Spain have been named in his honour. Casper also found out from an inconspicuous tiny note on an excursion drawing from the 16th century that the name *Pinguicula* had been created by Conrad Gessner (1516-65) using a plant from Mt. Pilatus near Lucerne. After both his wife and Jost became seriously ill, the Casper couple moved to Dresden, where they were looked after by relatives. With Jost Casper's death, Botany has lost a highly educated, spirited, obstinate, passionate and incredibly resilient scientist of international standing. His herbarium specimens are conserved at the Herbarium Haussknecht in Jena.

On the infrageneric classification of *Pinguicula*

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Keywords: taxonomy, butterworts, systematics, *Pinguicula*, classification.

Abstract: In this article, the morphology-based "traditional" infrageneric classification of the genus *Pinguicula* is opposed to "modern", phylogeny-based concepts. But concepts are compared and illustrated, and a new infrageneric concept of four sections for the Central American evolutionary linage of *Pinguicula* is proposed.

The genus *Pinguicula* comprises about 115 species currently recognized[1] (and several more named).

Three subgenera have been defined within the genus by Barnhart (1916), and many sections have been added to these later. This has been the outcome of morphological analyses, largely founded in the 1960s (Ernst 1961; Casper 1962, 1963, 1966). The three major subgeneric lineages were also confirmed by all recent molecular reconstructions of the genus' evolutionary history (Cieslak *et al.* 2005; Degtjareva *et al.* 2006; Beck *et al.* 2008; Fleischmann & Roccia 2018; Shimai *et al.* 2021). However, the circumscriptions of these three subgenera, that is which sections and species should belong into which subgenus, differ greatly between the morphologically defined approach and the molecular phylogenetic concepts. This led to two different "schools" and the usage of two largely incompatible classifications in recent publications dealing with the systematics and taxonomy of *Pinguicula*, one applying the morphological concept founded by Casper's work (Casper 1963, 1966), the other one following the phylogenetic approach. For the latter, a new infrageneric classification of *Pinguicula* in accordance with phylogenetic data has been proposed by Fleischmann & Roccia (2018). In the present article, both classifications for the genus are compared (see Figs. 1 & 2).

Pinguicula classifications – flowers or genes, what tells us the truth?

The "classic", morphology-based classification of the genus *Pinguicula* (see Fig. 1) largely considers flower characters to arrange the species in subgenera, sections, and even several ranks below (subsections and series). Casper (1962, 1963, 1966, 2019) considered of great taxonomic value the shape of the corolla (two-lipped=bilabiate or zygomorphic *versus* radiate=isolobate or actinomorphic), the length and shape of the corolla tube (funnel-shaped *versus* short and sack-like) and the spur (straight vs. curved, narrow and thin vs. short and sack-like, the angle the spur forms with the corolla tube, etc.), the presence and shape of a corolla throat (=palate), the pattern of hairs on the corolla interior (mainly: three rows of hair vs. different pattern), but also corolla color patterns. Casper also considered other characters for his classification, but

[1] The species concept used here is following Fleischmann & Roccia (2018). The species described past 2018 have been included here, with the exception of the Mexican *P. michoacana*, which is considered by the author part of the widespread *P. oblongiloba*, and the Cuban *P. baezensis* which is considered conspecific with *P. bissei*, and *P. moaensis*, which seems to be conspecific with *P. lippoldii*.

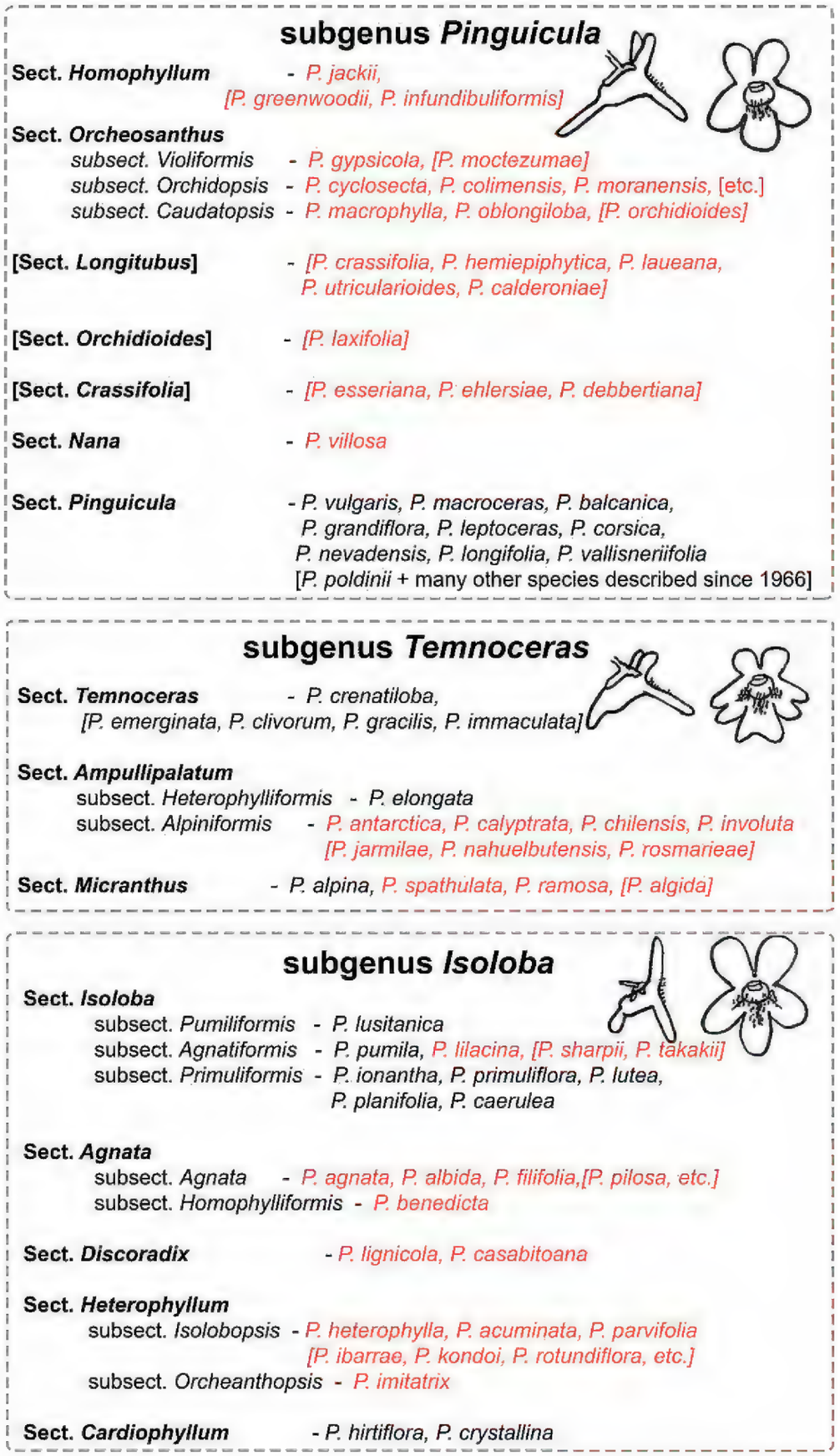
subgenus Pinguicula
Sect. Homophyllum - P. jackii,
[P. greenwoodii, P. infundibuliformis]
Sect. Orcheosanthus
subsect. Violiformis - P. gypsicola, [P. moctezumae]
subsect. Orchidopsis - P. cyclosecta, P. colimensis, P. moranensis, [etc.]
subsect. Caudatopsis - P. macrophylla, P. oblongiloba, [P. orchidioides]
[Sect. Longitubus] - [P. crassifolia, P. hemiepiphytica, P. laueana, P. utricularioides, P. calderoniae]
[Sect. Orchidioides] - [P. laxifolia]
[Sect. Crassifolia] - [P. esseriana, P. ehlersiae, P. debbertiana]
Sect. Nana - P. villosa
Sect. Pinguicula - P. vulgaris, P. macroceras, P. balcanica, P. grandiflora, P. leptoceras, P. corsica, P. nevadensis, P. longifolia, P. vallisneriifolia [P. poldinii + many other species described since 1966]
subgenus Temnoceras
Sect. Temnoceras - P. crenatiloba, [P. emerginata, P. clivorum, P. gracilis, P. immaculata]
Sect. Ampullipalatum
subsect. Heterophylliformis - P. elongata
subsect. Alpiniformis - P. antarctica, P. calyptrata, P. chilensis, P. involuta [P. jarmilae, P. nahuelbutensis, P. rosmarieae]
Sect. Micranthus - P. alpina, P. spathulata, P. ramosa, [P. algida]
subgenus Isoloba
Sect. Isoloba
subsect. Pumiliformis - P. lusitanica
subsect. Agnatiformis - P. pumila, P. lilacina, [P. sharpii, P. takakii]
subsect. Primuliformis - P. ionantha, P. primuliflora, P. lutea, P. planifolia, P. caerulea
Sect. Agnata
subsect. Agnata - P. agnata, P. albida, P. filifolia,[P. pilosa, etc.]
subsect. Homophylliformis - P. benedicta
Sect. Discoradix - P. lignicola, P. casabitoana
Sect. Heterophyllum
subsect. Isolobopsis - P. heterophylla, P. acuminata, P. parvifolia [P. ibarrae, P. kondoi, P. rotundiflora, etc.]
subsect. Orcheanthopsis - P. imitatrix
Sect. Cardiophyllum - P. hirtiflora, P. crystallina

Figure 1: "Traditional", morphology-based classification of the genus *Pinguicula*, following Casper (1962, 1963, 1966) and Casper & Stimper (2009). In that system, the subgenus division is mainly based on the coloration and shape of the corolla (thumbnail images). Sections and species that were added after Casper's monograph (Casper 1966) by various authors are in square parentheses, but not all new species are added here. In red are conflicting species that do not fall in the respective subgenera in any of the phylogenetic reconstructions (see Fig. 2).

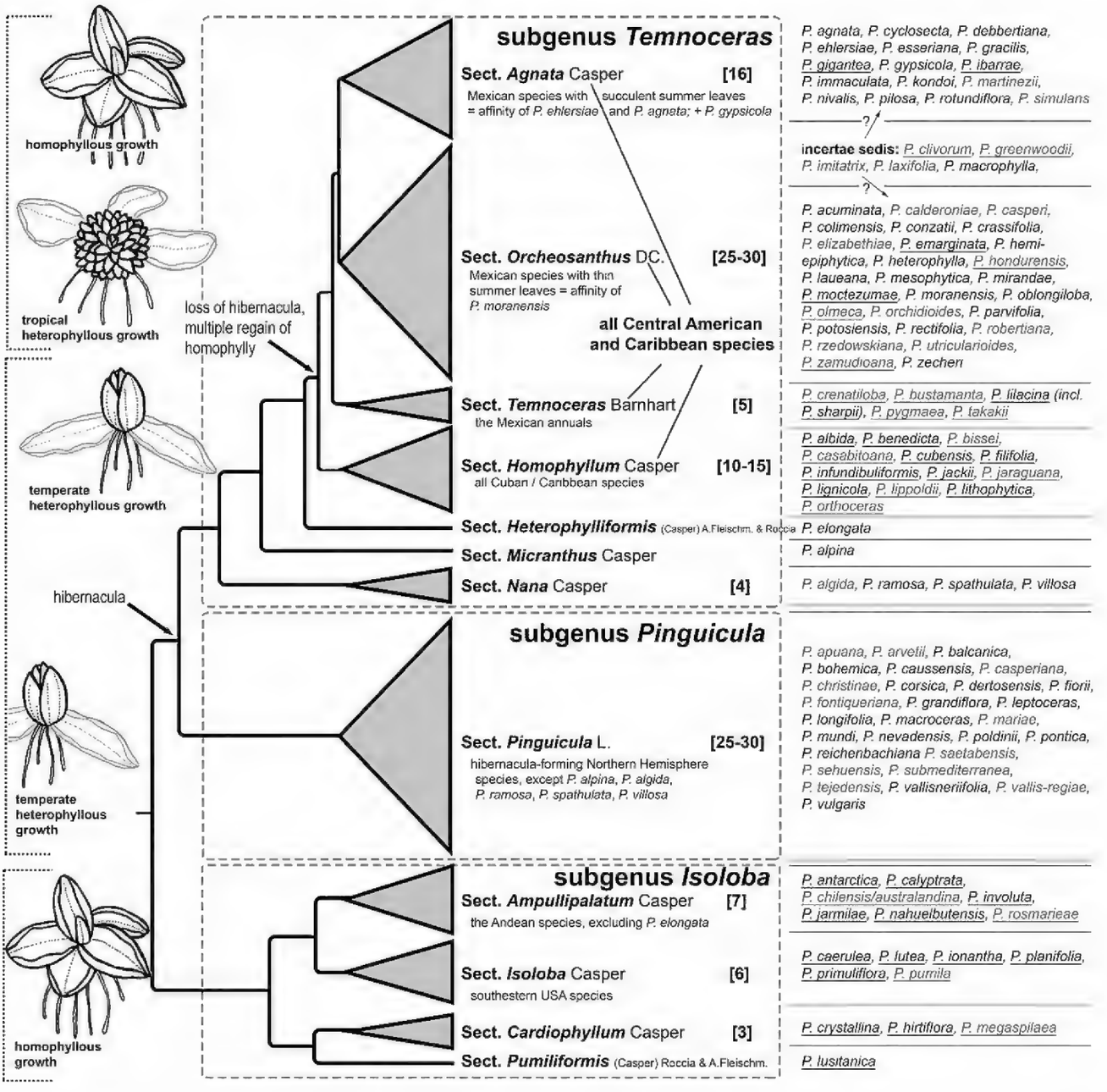
homophyllous growth
tropical heterophyllous growth
loss of hibernacula, multiple regain of homophylly
temperate heterophyllous growth
hibernacula
temperate heterophyllous growth
homophyllous growth
subgenus Temnoceras
Sect. Agnata Casper [16]
Mexican species with succulent summer leaves = affinity of P. ehlersiae and P. agnata; + P. gypsicola
Sect. Orcheosanthus DC. [25-30]
Mexican species with thin summer leaves = affinity of P. moranensis
all Central American and Caribbean species
Sect. Temnoceras Barnhart [5]
the Mexican annuals
Sect. Homophyllum Casper [10-15]
all Cuban / Caribbean species
Sect. Heterophylliformis (Casper) A.Fleischm. & Roccia
Sect. Micranthus Casper
Sect. Nana Casper [4]
subgenus Pinguicula
Sect. Pinguicula L. [25-30]
hibernacula-forming Northern Hemisphere species, except P. alpina, P. algida, P. ramosa, P. spathulata, P. villosa
subgenus Isoloba
Sect. Ampullipalatum Casper [7]
the Andean species, excluding P. elongata
Sect. Isoloba Casper [6]
southestern USA species
Sect. Cardiophyllum Casper [3]
Sect. Pumiliformis (Casper) Roccia & A.Fleischm.
P. agnata, P. cyclosecta, P. debbertiana, P. ehlersiae, P. esseriana, P. gracilis, P. gigantea, P. gypsicola, P. ibarrae, P. immaculata, P. kondoi, P. martinezii, P. nivalis, P. pilosa, P. rotundiflora, P. simulans
incertae sedis: P. clivorum, P. greenwoodii, P. imitatrix, P. laxifolia, P. macrophylla,
P. acuminata, P. calderoniae, P. casperi, P. colimensis, P. conzatii, P. crassifolia, P. elizabethiae, P. emarginata, P. hemiepiphytica, P. heterophylla, P. hondurensis, P. laueana, P. mesophytica, P. mirandae, P. moctezumae, P. moranensis, P. oblongiloba, P. olmeca, P. orchidioides, P. parvifolia, P. potosiensis, P. rectifolia, P. robertiana, P. rzedowskiana, P. utricularioides, P. zamudioana, P. zecheri
P. crenatiloba, P. bustamanta, P. lilacina (incl. P. sharpii), P. pygmaea, P. takakii
P. albida, P. benedicta, P. bissei, P. casabitoana, P. cubensis, P. filifolia, P. infundibuliformis, P. jackii, P. jaraguana, P. lignicola, P. lippoldii, P. lithophytica, P. orthoceras
P. elongata
P. alpina
P. algida, P. ramosa, P. spathulata, P. villosa
P. apuana, P. arvetii, P. balcanica, P. bohemica, P. caussensis, P. casperiana, P. christinae, P. corsica, P. dertosensis, P. fiorii, P. fontiqueriana, P. grandiflora, P. leptoceras, P. longifolia, P. macroceras, P. mariae, P. mundi, P. nevadensis, P. poldinii, P. pontica, P. reichenbachiana P. saetabensis, P. sehuensis, P. submediterranea, P. tejedensis, P. vallisneriifolia, P. vallis-regiae, P. vulgaris
P. antarctica, P. calyptrata, P. chilensis/australandina, P. involuta, P. jarmilae, P. nahuelbutensis, P. rosmarieae
P. caerulea, P. lutea, P. ionantha, P. planifolia, P. primuliflora, P. purrila
P. crystallina, P. hirtiflora, P. megaspilaea
P. lusitanica

Figure 2: Phylogeny-based classification of *Pinguicula*, adopted from Fleischmann & Roccia (2018). The clade of Central American species, considered a single section *Temnoceras* by them is here split further into four sections, reflecting the phylogenetic results by Shimai (2017) and Shimai *et al.* (2021). This classification mirrors the evolutionary history of the genus, with every monophyletic terminal lineage treated as a section. The widths of the triangles correspond to species numbers given in square brackets. Species that have not yet been included in phylogenetic reconstructions in grey, these are assigned to the respective sections based on postulated affinities or morphological similarities. Underlined species names = homophyllous growth.

he rated the floral characters by far the highest value: "*The character complex of the flower is complemented by the taxonomically 'valuable' characters of growth form, chromosome number, life form and distribution.*" (Casper 1966, p. 59, literally translated from the German original). Casper further explains that "*the character complex flower can serve as 'standard' for the evaluation of the genealogical connections, as it did not undergo any or just indiscernible functional changes* [during evolution]. *All remaining characters can be measured with it.*" (Casper 1966, p. 59). However, Casper's assumption of "floral functional stability" has proven fundamentally wrong in the light of evolutionary concepts, as certain flower characters can be switched quickly during evolution in adaptation to new pollinator groups or when new floral syndromes evolve, especially in young evolutionary lineages that are still in the process of biological radiation – this holds true for any group of plants, including *Pinguicula* (Cieslak *et al.* 2005; Fleischmann 2016; Fleischmann & Roccia 2018; Lustofin *et al.* 2020; Shimai *et al.* 2021). This can result in closely related species displaying quite different, diverging floral morphology (= divergent evolution), but also in rather distantly related species that show strikingly similar flower shapes (= convergent or parallel evolution) – both can be visualized in Figure 3. An example of the former case is that of the two closely related Mexican species *Pinguicula gracilis* and *P. rotundiflora* (both have rosettes that are very similar, both share a similar habitat and distribution range, and both can easily be hybridized in cultivation; pers. obs.). However, both apparently adapted to quite different pollinators, as the former species shows a distinctly two-lobed corolla, with a large corolla lower lip and a comparatively small upper lip. *Pinguicula rotundiflora*, as already its name implies, has an isolobate corolla, i.e., a radiate flower in which all five petals are almost the same length. This led Casper and others (Studnička 1985; Zamudio 1988; Casper & Stimper 2009) to the conclusion that the two species should belong to two different subgenera, based on the divergent flower shapes, i.e., they were considered not to be closely related: *P. gracilis* was either placed in *P.* subgenus *Temnoceras* section *Temnoceras* (Zamudio 1988) or in the newly created *P.* section *Microphyllum* of subgenus *Temnoceras* (Luhrs & Lampard 2006; Casper & Stimper 2009) based on its two-lipped corolla, while *P. rotundiflora* was put in *P.* subgenus *Isoloba* section *Isolobopsis* because of its radiate corolla (Fig. 1). However, all molecular phylogenetic studies that included these two taxa independently show that both are closely related sister species (Shimai & Kondo 2007; Lustofin *et al.* 2020; Shimai *et al.* 2021), which exposes their different subgeneric/sectional classification based on flower morphology as artificial, so it does not mirror their natural affinity. There are several more examples where morphology-based concepts and phylogenetic results are in conflict. Hence, we need to have a closer look at both concepts here in order to understand why there is some discordance regarding the placement of some species in the respective sections and subgenera.

Casper (1963, 1966) circumscribed the three subgenera as follows:

***P.* subgenus *Isoloba* Barnhart** comprised species with radiate (isolobate), 5-merous corolla (but Casper also included here a few species with bilabiate corolla, such as the Cuban *P. benedicta*), with the petals more or less equal in size, the hairs of the corolla tube arranged in three rows, and flowers containing some yellow-colored parts. This section, according to Casper (1966) only comprised species of tropical growth type, i.e., such that only form a single type of carnivorous leaves but do not form winter rosettes.

***P.* subgenus *Temnoceras* Barnhart** included species with two-lipped corolla with a well-expressed corolla lower lip that has its middle lobe larger than the lateral ones, and with the lobes of the corolla lower lip distinctly notched (crenate), with unequal petals (those of the upper corolla

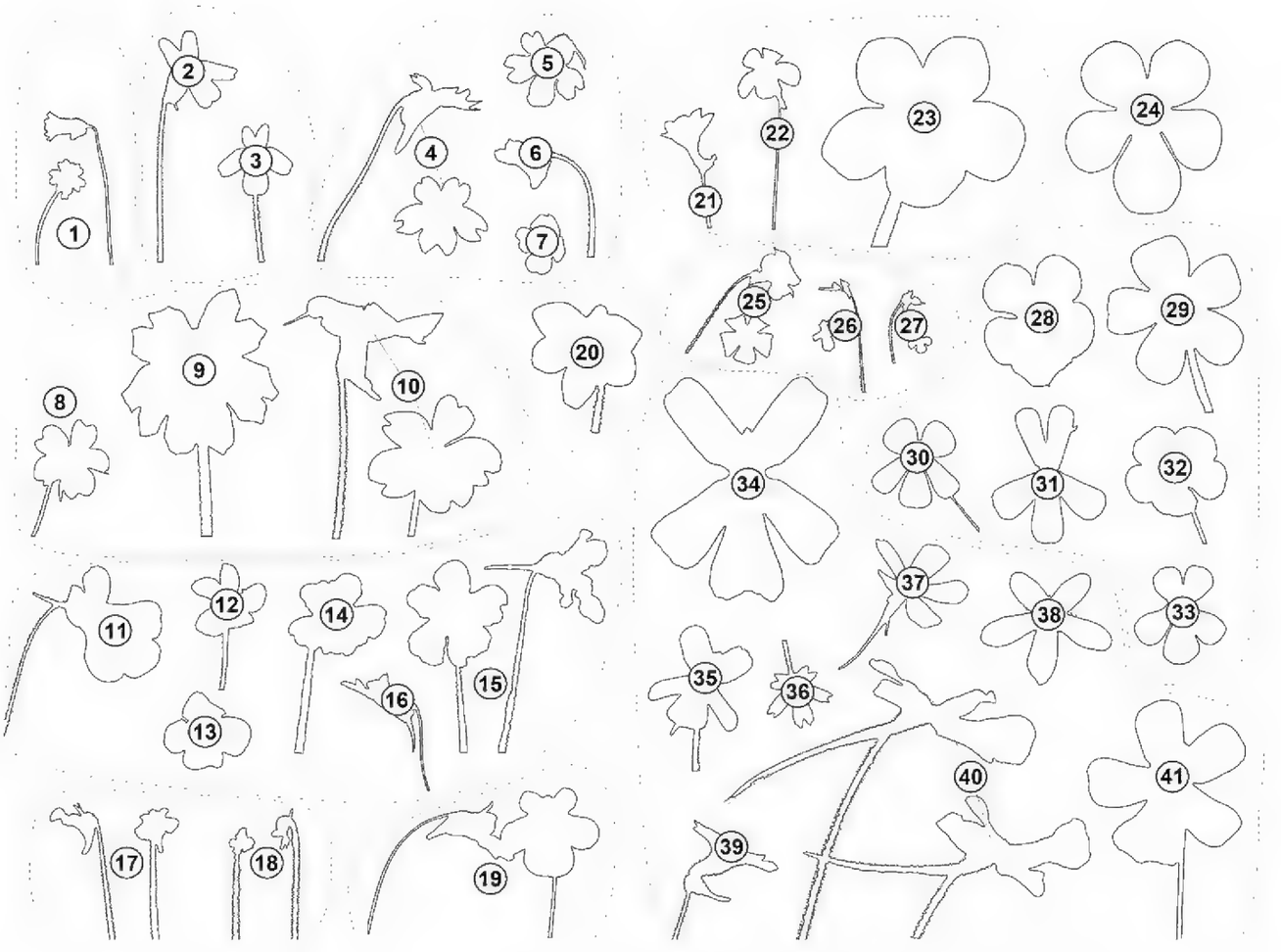

Figure 3: (preceding facing pages). Flower diversity in the genus *Pinguicula*. All flowers approximately to the same scale. Species arranged by phylogenetic affinity. *P.* section *Pumiliformis:* **1.** *P. lusitanica*. Section *Cardiophyllum:* **2.** *P. hirtiflora*, **3.** *P. crystallina*. Section *Ampullipalatum:* **4.** *P. jarmilae*, **5.** *P. calyptrata*, **6.** *P. antarctica*, **7.** *P. nahuelbutensis*. Section *Isoloba:* **8.** *P. pumila*, **9.** *P. lutea*, **10.** *P. primuliflora*. Section *Pinguicula:* **11.** *P. longifolia*, **12.** *P. corsica*, **13.** *P. leptoceras*, **14.** *P. grandiflora* subsp. *rosea*, **15.** *P. grandiflora* subsp. *grandiflora*, **16.** *P. vulgaris*. Section *Nana:* **17.** *P. spathulata*, **18.** *P. villosa*. Section *Micranthus:* **19.** *P. alpina*. Section *Heterophylliformis:* **20.** *P. elongata*. Section *Homophyllum:* **21.** *P. cubensis*, **22.** *P. filifolia*, **23.** *P. jackii*. Not assigned to any section yet: **24.** *P. laxifolia*. Section *Temnoceras:* **25.** *P. lilacina*, **26.** *P. crenatiloba*, **27.** *P. pygmaea*. Section *Agnata:* **28.** *P. cyclosecta*, **29.** *P. agnata*, **30.** *P. debbertiana*, **31.** *P. gypsicola*, **32.** *P. kondoi*, **33.** *P. esseriana* 'white flower'. Section *Orcheosanthus:* **34.** *P. moranensis*, **35.** *P. moranensis 'rosei'*, **36.** *P. emarginata*, **37.** *P. crassifolia*, **38.** *P. parvifolia*, **39.** *P. mirandae*, **40.** *P. laueana* 'Geranium flower', **41.** *P. laueana* 'Sierra Mixe'. Photos of *P. calyptrata* and *P. pygmaea* by Fernando Rivadavia, of *P. elongata* by Sebastian Vieira, of *P. antarctica*, *P. crenatiloba*, *P. lilacina*, *P. lutea*, *P. pumila*, and *P. villosa* by Markus Welge, all other photos and image composition by A. Fleischmann.

lip much shorter), the tube hairs in three rows, and the corolla usually containing yellow colors. This section comprises species of tropical and temperate growth type (i.e., forming winter rosettes or hibernacula).

***P.* subgenus *Pinguicula* L.** covered species with a two-lipped corolla in which the lobes are always entire, and in which the corolla does not contain any yellow colors (according to Casper 1966, the only exception in that subgenus is *P. villosa*), with the tube hairs not arranged in three rows, encompassing species of tropical and temperate growth type.

However, with the discovery of new species, but also as we gained more information about the natural variation of some *Pinguicula* species, it got more and more difficult to maintain Casper's above-mentioned generic classification, as certain species did not fit well any of the morphologically defined subgenera, while others showed so much infraspecific variation that they would easily fall into at least two of the subgenera. The sections put up by Casper (1962, 1963, 1966) to encompass the known *Pinguicula* species were likewise not sufficient anymore with the discovery of new, quite distinctive species. Some authors were uncertain where to place their new discoveries in Casper's system and left that question unanswered, or created new sections in order to fit their species. For example, Luhrs (1995) coined *P.* section *Orchidioides* exclusively for his new *P. laxifolia*, suggesting that this species was quite isolated and not closely related with any of the other known species. As we know today, this species belongs to a single evolutionary lineage that includes all Mexican and Central American species (= *P.* section *Temnoceras sensu* Fleischmann & Roccia 2018). This is confirmed by the fact that *P. laxifolia* forms natural hybrids with a small-flowered form of *P. esseriana* that is sympatrically growing at the El Cielo mountains (Salinas-Rodriguez *et al.* 2019), thus it cannot be evolutionarily isolated. Zamudio & Rzedowski (1991) added a new *P.* section *Longitubus* for those *Pinguicula* species with very long corolla tubes and long spurs (such as *P. crassifolia*, *P. hemiepiphytica*, and *P. laueana*; see Fig. 3). Certainly, these long-spurred, funnel-tubed flowers (which additionally show bright red, purple, or magenta colors) evolved in these species in adaptation to hummingbird pollination (Lampard *et al.* 2016; Lustofin *et al.* 2020). And obviously *P. laueana* and *P. hemiepiphytica* are much more closely related to *P. moranensis* (which, based on the morphological concept, was placed in a different section, *P.* section *Orchidopsis*), than they are to the other species (*P. crassifolia*, *P. utricularioides*, *P. calderoniae*) they have been associated with in section *Longitubus*. The morphological classification also shows other inconsistencies. For example, Speta & Fuchs (1982) put up a new section *Crassifolia* within *P.* subgenus *Pinguicula* in which they placed three of the Mexican species with very succulent leaves (*P. debbertiana*, *P. ehlersiae*, *P. esseriana*), while the likewise succulent *P. gracilis*, *P. nivalis*, and *P. immaculata* were retained by their respective authors in *P.* subgenus *Pinguicula* section *Temnoceras*, or in a newly coined *P.* section *Microphyllum* of subgenus *Temnoceras* (Luhrs & Lampard 2006; Casper & Stimper 2009), whereas the vegetatively almost identical, succulent species *P. kondoi* and *P. rotundiflora* were maintained even in a different subgenus – in *P.* subgenus *Isoloba* section *Isolobopsis* – just because of their different corolla shapes. Needless to say that all above-mentioned succulent Mexican species can be artificially hybridized (pers. obs.; many of these hybrids are found in CP growers' collections today), showing no cross-fertility borders and hence suggesting close relationship. Indeed, molecular phylogenies (Shimai 2017; Shimai *et al.* 2021) revealed *P. esseriana*, *P. ehlersiae*, *P. gracilis*, *P. immaculata*, *P. nivalis*, *P. rotundiflora*, and *P. kondoi* (the latter under the name *P. reticulata*) as closely related species: they all fall in the same clade, i.e., they comprise a single evolutionary lineage that evolved from a common ancestor.

Casper's weight on flower colors also had to be questioned with the discovery of new species, or variation within species. According to Casper (1966), members of *P.* subgenus *Pinguicula* (except *P. villosa*) lack any yellow color on the corolla – however, several local forms of Mexican species that were placed in that subgenus do present some yellow on the corolla tube or palate, e.g., some forms of *P. moranensis*, *P. laueana*, or *P. esseriana* (see Fig. 3). On the other hand, Casper (1963, 1966) defined *P.* subgenus *Temnoceras* for species that usually include some yellow color on their flowers. However, with the addition of *P. jarmilae* (syn. *P. chuquisacensis*) to the very natural group

of the Andean species (=*P.* section *Ampullipalatum*, which is a monophyletic lineage, if *P. elongata* is excluded, as the latter belongs the lineage of the Central American species; Beck *et al.* 2008) that concept did not fit anymore, as *P. jarmilae* does not show any trace of yellow on its corolla. In that case, Casper (pers. com. 2017) admitted that this species should belong to *P.* section *Ampullipalatum*, but that his color concept had to be re-evaluated.

To sum it up: the infrageneric concept which largely was based on flower morphology does in several cases not mirror the natural affinities but divides related species into different sections or even subgenera, whereas in other cases, only distantly related species are artificially grouped together.

All three subgenera as defined by Casper (1966), and all but one of his morphologically circumscribed sections were retrieved as para- and polyphyletic in all of the molecular phylogenies. 'Paraphyletic' means that a defined group also comprises species that were previously classified as belonging to other groups: for example, Casper's *P.* section *Isoloba* (which is by definition the evolutionary lineage (=clade) that comprises the section's type species – for *Isoloba* this is *P. pumila*) included species from various lineages (corresponding to *P.* subgenus *Isoloba* and *P.* subgenus *Temnoceras sensu* Fleischmann & Roccia 2018) in phylogenetic reconstructions (Cieslak *et al.* 2005; Degtjareva *et al.* 2006; Shimai *et al.* 2021). 'Polyphyletic' means that members of a defined group that was thought to be a natural evolutionary lineage show up in different places (clades) in the phylogenetic tree. For example, what Casper (1963, 1966) circumscribed as *P.* subgenus *Pinguicula* phylogenetically divided into two subgenera: *P.* subgen. *Pinguicula* and *P.* subgen. *Temnoceras* and into four sections (*P.* sections *Pinguicula*, *Orcheosanthus*, *Agnata*, and *Homophyllum*, as reclassified here). The contrary would be 'holophyletic', i.e., that after phylogenetic analysis, an identified lineage still contains all members originally assigned to one named group and excludes all members originally placed in different groups (of comparable rank), and 'monophyletic', i.e., that all members of a named group indeed belong to a common evolutionary lineage (clade), i.e., they were all derived from a single common ancestor. In the case of the butterworts, only *P.* section *Pinguicula* (that is the temperate, hibernacula forming species excluding *P. alpina*, *P. ramosa*, *P. spathulata*, *P. algida*, and *P. villosa*) as defined by Casper (1962, 1963, 1966) was found to be monophyletic in all phylogenetic reconstructions.

However, it is important to mention that molecular phylogenies also cannot be considered the 'single, final truth'. These family trees should rather be considered hypotheses that try to reconstruct the evolutionary history of a group of plants as best as possible. The quality of a phylogeny depends on many factors, most importantly a complete taxon sampling (the more of the known species are included, the closer the phylogenetic tree will come to the evolutionary history of a genus; of course, nobody is able to tell about the lineages and species that got extinct during the millions of years of evolution without leaving fossil remnants, and it is almost impossible to predict what taxa will be discovered and described in future). Depending on the genetic markers used, the respective phylogenetic reconstructions may show incongruences between nuclear (inherited by both parents) and plastid (inherited only by a single parent, in most plants by the mother lineage) marker data.

The molecular phylogeny-based classification is in accordance with growth form (Fig. 2), and also largely mirrors geography (Cieslak *et al.* 2005; Beck *et al.* 2008; Fleischmann & Roccia 2018; Shimai *et al.* 2021). Based on phylogenetic results, Fleischmann & Roccia (2018) proposed a new infrageneric classification of *Pinguicula*, in which the three major clades correspond to the three subgenera, and all subclades were defined as sections (Fig. 2).

Further subdivision of *P.* section *Temnoceras*, the Mexican and Caribbean butterworts

All Central American and Caribbean *Pinguicula* species were retrieved as a monophyletic lineage in all phylogenetic reconstructions (Degtjareva *et al.* 2006; Shimai *et al.* 2007; Kondo & Shimai 2007). Therefore, Fleischmann & Roccia (2018) united them in a single, large *P.* section *Temnoceras* that comprises ca. 60 species. However, Shimai *et al.* (2021) in their large-scale phylogeny retrieved four well-supported subclades within that lineage: one comprising all Caribbean species, one covering the Mexican annuals (represented by *P. lilacina* and *P. sharpii* in their phylogeny, two taxa which however are considered conspecific by Lampard *et al.* 2016, Roccia *et al.* 2016, and Rivadavia *et al.* 2017, and which are even given as synonyms in Appendix S1 of Shimai *et al.* 2021). Another lineage covers the species with very succulent carnivorous leaves with margins involute only near the very tip or not involute at all, i.e., the relatives of *P. agnata* and of *P. esseriana*, and additionally *P. gypsicola* was found in that group by Shimai *et al.* (2021). However, also *P. macrophylla* was retrieved among those species in the analyses of Shimai *et al.* (2021), which one would rather assume in the fourth clade, comprising all the species with larger, thinner carnivorous leaves with leaf margins involute along their lateral margins, i.e., *P. moranensis* and allies, but also *P. moctezumae* and *P. heterophylla* with upright, thread-like leaves and revolute margins (a habit similar to that of *P. gypsicola*). Following the infrageneric classification of Fleischmann & Roccia (2018), these four subclades of Shimai *et al.* (2021) might be considered subsections within a monophyletic *P.* section *Temnoceras*. However, that would have necessitated several new combinations and the rejection of well-established names for some of the Mexican lineages. Hence these four subclades are here considered four sections (see Fig. 2) for what Fleischmann & Roccia (2018) treated as a single one (*P.* section *Temnoceras*).

Some of the clades have already been given names at the rank of section by Shimai (2017), however unfortunately, these names are not validly published as they were published in a PhD thesis, which does not constitute a nomenclaturally effective publication according to the Code of Nomenclature (ICN Art. 30.9; Turland *et al.* 2018). Even if the newly proposed section names of Shimai (2017) had been published effectively, in order to be validly published all clades recognized by them would have required the usage of the oldest available name at the rank of section, if a member in any clade was the type of any previously defined section. Additionally, those new combinations made by Shimai (2017) that were based on Casper's (1966) earlier subsectional and series names are not validly published because no basionym reference was given (ICN Art. 41.5). Therefore, new section circumscriptions are proposed here for those lineages (clades) that thus far have not been correctly assigned to any named group in the genus *Pinguicula*.

P. subgenus *Temnoceras* section *Homophyllum* Casper (1963: 325)
Type species: *P. jackii* Barnhart
= *P.* section *Discoradix* Casper
= *P.* subsection *Homophylliformis* Casper
= *P.* subsection *Agnata* Casper, p.p. (*P. albida*, *P. filifolia*)
= *P.* section *Caribensis* Shimai, nomen

The oldest available names for a group comprising the Caribbean species, i.e., corresponding to the Cuban lineage or 'Clade IX' of Shimai *et al.* (2021) are *P.* subsection *Homophylliformis* (put up by Casper (1966) for *P. benedicta*) and *P.* section *Homophyllum* (*sensu* Casper

1963, 1966 encompassing only *P. jackii*; other species from Mexico have been added by different authors later, see Fig. 1). Casper (1966) placed the remainder of the Cuban species with radiate corolla into *P.* section *Agnata* subsection *Agnata* (together with the Mexican species *P. agnata*). Later, Casper & Stimper (2009) suggested to transfer *P. albida* into *P.* section *Isoloba*. The name *P.* section *Homophyllum* is chosen here for the Cuban evolutionary lineage, as it is the oldest available one for that lineage at the rank of section. It is transferred from *P.* subgenus *Pinguicula*, where it was placed by Casper, to *P.* subgenus *Temnoceras*, in accordance with the phylogenetic topology (Shimai *et al.* 2007; Shimai 2017; Shimai *et al.* 2021). In later works, Casper himself considered the placement of *P. jackii* in his section *Homophyllum* separated from the other Cuban taxa, an unsatisfactory makeshift (Casper & Stimper 2009) or even "incorrect" (Casper 2019: 116) and explained it to have been based on poor knowledge on the actual relationships of *P. jackii*, a species he previously considered to be quite isolated within the genus. With the new circumscription of Casper's section *Homophyllum* as *P.* subgenus *Temnoceras* section *Homophyllum*, that lineage will not only encompass *P. jackii*, but it contains all Caribbean *Pinguicula* species, in accordance with phylogenetic data that show the monophyly of the Cuban taxa (Shimai *et al.* 2007; Shimai *et al.* 2021; unpublished ITS data cited in Casper 2019: 117). Casper's section *Discoradix*, which he put up for the two epiphytic species with modified anchoring roots (*P. lignicola* and *P. casabitoana*) fully falls into that lineage as well, as evidenced by phylogenetic analyses (Shimai *et al.* 2007; Shimai *et al.* 2021).

P. subgenus *Temnoceras* Barnhart (1916: 46) section *Temnoceras*
Type species: *P. crenatiloba* DC.
= *P.* subsection *Agnatiformis* Casper, p.p. (*P. lilacina*)
= *P.* section *Membraniformis* Shimai, nomen

This section, as redefined here (different from the usage by Fleischmann & Roccia 2018), includes the Mexican annuals, which are delicate species with thin, membranous leaves. The autonymous type section of subgenus *Temnoceras* by definition is the lineage that includes the type species of that subgenus, i.e., *P. crenatiloba*. Although that species had not been included in any phylogenetic analyses yet, it is evidently closely related to the other delicate Mexican annuals, *P. lilacina*, *P. takakii*, and *P. pygmaea* (Rivadavia *et al.* 2017). Clade VI of Shimai *et al.* (2021) covers these annual species, represented in their sampling by *P. lilacina* and *P. sharpii*, or respectively, by two accessions of *P. lilacina* if you consider both species conspecific (Lampard *et al.* 2016; Rivadavia *et al.* 2017). Based on morphological similarities (Rivadavia *et al.* 2017), *P. crenatiloba* is likely to fall into that clade as well.

The phylogenetic position of the newly discovered *P. bustamanta* (Zamudio & Nevárez-de los Reyes 2020) has not been revealed yet, however it is here tentatively placed in *P.* subgenus *Temnoceras* section *Temnoceras* (in accordance with Zamudio & Nevárez-de los Reyes 2020, who placed it in *P.* section *Isoloba* subsection *Agnatiformis* (*sensu* Casper 1966), suggesting a close affinity to *P. lilacina*). Indeed, *P. bustamanta*, although a perennial, fits well morphologically the remainder of the annual species of *P.* section *Temnoceras*. Interestingly, the perennial homophyllous habit of *P. bustamanta* with its thin membranous leaves seems to link it to the Cuban species of *P.* section *Homophyllum*, to which *P.* section *Temnoceras* is the consecutive sister lineage in the phylogenetic tree (Fig. 2; Shimai *et al.* 2021). The overall habit, as well as flower morphology of *P. bustamanta* are indeed strongly reminiscent of some of the Cuban species, most notably *P. jackii* and *P. lithophytica* – and coincidentally, these

three limestone-dwelling lithophytic species are unique within the genus in having leaves with a row of long-stalked glandular hairs present on the midrib on the lower (abaxial) leaf surface. It would be highly desirable to include *P. bustamanta* in molecular phylogenetic analyses of the genus. In case it will turn out as early-branching taxon within *P.* section *Temnoceras*, this would confirm the postulated theory of a surviving 'missing link' between the Caribbean and Mexican lineages of *Pinguicula* (see e.g., Casper 2019), i.e., between sections *Homophyllum* and *Temnoceras*.

P. subgenus *Temnoceras* section *Orcheosanthus* DC. (1844: 27)
Type species: *P. moranensis* Kunth
= *P.* section *Heterophyllum* Casper
= *P.* section *Longitubus* Zamudio & Rzed.
= *P.* subsection *Orchidopsis* Casper, p.p. (*P. moranensis*, *P. colimensis*)
= *P.* subsection *Caudatopsis* Casper p.p. (*P. oblongiloba*)
= *P.* subsection *Infundibulares* Zamudio & Rzed.
= *P.* subsection *Utricullariopsis* Zamudio & Rzed.
= *P.* section *Mesoamericana* Shimai, nomen, nom. superfl.

DeCandolle (1844) put up the oldest available name at the rank of section for the clade comprising *P. moranensis*, which corresponds to Clade VII of Shimai *et al.* (2021). This is also the taxonomic name most frequently used in the literature for the group of large, 'orchid-flowered' Mexican butterworts (e.g., Zamudio 2001; Casper & Stimper 2009) which belong to that evolutionary lineage.

P. subgenus *Temnoceras* section *Agnata* Casper (1963: 331), emend. A.Fleischm.
Type species: *P. agnata* Casper
= *P.* section *Crassifolia* Speta & F.Fuchs
= *P.* section *Microphyllum* Luhrs
= *P.* subsection *Agnata* Casper, p.p. (*P. agnata*)
= *P.* subsection *Violiformis* Casper
= *P.* subsection *Orchidopsis* Casper, p.p. (*P. cyclosecta*)

The newly circumscribed *P.* section *Agnata* excludes the Cuban species which Casper (1966) assigned to that section (*P. albida*, *P. filifolia*, *P. benedicta*). These are now all included in *P.* section *Homophyllum*. *Pinguicula* section *Agnata* as recircumscribed here includes all Mexican species with succulent summer leaves, i.e., the relatives of *P. agnata*, *P. esseriana* (= those species previously classified in section *Crassifolia*), and those of *P. gracilis* (= species previously included in section *Microphyllum*). Additionally, it includes *P. gypsicola* which, although a species with membranous, filiform summer leaves, seems to be derived from ancestors with succulent summer leaves, judging from its phylogenetic position (Shimai *et al.* 2021). It would be interesting to reinvestigate the phylogenetic position of *P. macrophylla*, which turned up in the same clade as the succulent-leaved species in the analysis of Shimai *et al.* (2021), although it would morphologically indicate a closer relationship with *P.* section *Orcheosanthus* (see Casper 1966; Zamudio 2001).

The two section names chosen here for the two evolutionary lineages of perennial Mesoamerican *Pinguicula* species might fit Casper's later view on that group, which he referred to as "the Central American *Orcheosanthus* and *Agnata* species groups" (Casper 2019: 110).

For biological reasons, it might have been better to choose subsections, not sections, to name the four lineages of Mexican and Caribbean species (as retrieved by Shimai *et al.* 2021) because the Mexican and Cuban species are interfertile (see below), while between the sections as circumscribed by Fleischmann & Roccia (2018), there are fertility-barriers, as explained further below. Also, the Mexican species all seem to be interfertile: this is well-known for the two clades defined here as sections *Orcheosanthus* and *Agnata*, as numerous artificial hybrids (and cultivars) exist that have been created between species that fall into these two sections (e.g., *P.* × 'Weser' and *P.* × 'Sethos', which involve crosses between *P. moranensis* of section *Orcheosanthus* and *P. ehlersiae* of section *Agnata*, but there are many more examples of such Mexican inter-section hybrids made by talented butterwort breeders). The annual members of *P.* section *Temnoceras* with their delicate flowers are apparently also interfertile with the remainder of Mexican species (that often exhibit very different flower morphologies), as is evident from the discovery of a natural hybrid between *P. takakii* (section *Temnoceras*) and *P. gypsicola* (section *Agnata*) by F. Rivadavia (Rivadavia 2003).

Pinguicula systematics and hybridization – can I create any imaginable butterwort hybrid?

One interesting "side-effect" of the phylogeny-based classification by Fleischmann & Roccia (2018), in which all subgenera and sections represent monophyletic evolutionary lineages, is that it apparently reflects well the cross-compatibility borders: within a given section, all species can be (artificially) hybridized with each other, no matter of geography (at least I do not know of any example that shows the contrary, but of a lot of examples which confirm this theory; by the way, the same holds true for *Drosera* hybridization and the phylogeny-based classification of *Drosera*). For example, all Mexican *Pinguicula* species (which all belong to a large *P.* section *Temnoceras* in the concept of Fleischmann & Roccia 2018) can hybridize, at least in cultivation, and also the Mexican and Cuban species can be hybridized with each other (I made the hybrid between the Cuban *P. jackii* and Mexican *P. agnata*, and on the internet, there are trustworthy photographs that show the putative hybrid of *P. moctezumae* and *P. filifolia*).

The "stand-alone" species of the monotypic sections *Micranthus* (*P. alpina*), *Heterophylliformis* (*P. elongata*) and *Pumiliformis* (*P. lusitanica*) cannot be hybridized with any other *Pinguicula* species (pers. obs.). And for the same reason, it will not be possible to create an artificial hybrid between a member of the *P. hirtiflora* complex (*P.* section *Cardiophyllum*) and one of the hibernacula-forming temperate species of *P.* section *Pinguicula* (I have tried doing so many times without success), or any *Pinguicula* species from any other section.

There is a single report of what would represent the rare case of an inter-sectional (and in fact also across-subgenus) hybrid in *Pinguicula*: Wettstein (1919) described a pollen-sterile, pale lilac-flowered putative natural hybrid between *P. alpina* and *P. vulgaris* (both which belong to different subgenera and sections) which he named as P. × *hybrida*. That hybrid is repeatedly mentioned in the literature (e.g., Ernst 1961; Casper 1966). But apart from the three herbarium specimens that comprise the historic type collection from Lower Austria south of Vienna, one collection from Finland and one from Slovakia (Casper 1966), that hybrid has never been relocated, despite the fact that both putative parent species are often found growing in close proximity in the European Alps. In my opinion, the identity of that hybrid is highly doubtful, and its description was probably based on pale-flowered forms of *P. vulgaris*, which are more or less frequent among normally-colored individuals in many European populations of that species (pers. obs.). Interestingly, the flower of the putative hybrid as depicted by Wettstein (1919) is

notably smaller than those of both parent species, and rather matches that of *P. vulgaris* in overall shape and morphology. From a phylogenetic perspective, that hybrid is unlikely to exist, and *P. alpina* and *P. vulgaris* are apparently cross-incompatible: despite having tried to artificially hybridize both species for more than 20 years (almost every season both species are in flower at the same time in my garden), I have never obtained even a single hybrid seed grain, but just got aborted seed capsules, no matter which way round I tried to perform that cross. Curiously, that putative hybrid was apparently once grown in cultivation from unknown source by the late German CP grower Uwe Westphal (pers. coms; I have never seen his plant personally, thus I cannot confirm or reject its identity).

Acknowledgements: The late Jost Casper, Aymeric Roccia, Fernando Rivadavia, Jan Schlauer, Julian Hernández, Sergio Zamudio, Maurizio Saroldi, Oliver Gluch, for correspondence on *Pinguicula* taxonomy over the past decades. Markus Welge, Kamil Pasek, Eric Partrat, Maurizio Saroldi, Klaus Keller, Stefan Ippenberger, and Paul Debbert for sharing some of their cultivated *Pinguicula* treasures with me. Jan Schauer and John Brittnacher are thanked for helpful comments on the manuscript.

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First record of overlap between two species of *Pinguicula* in the Andean Patagonian forest

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Keywords: Carnivorous plants, overlap, *Pinguicula australandina*, *Pinguicula antarctica*.

Abstract: In Argentina there are two species of carnivorous plants of the genus *Pinguicula*, *P. antarctica*, and *P. australandina*. These species, also present in Chile, have a distribution in Argentina limited to the Andean Patagonian Forest ecoregion, which ranges from southern Neuquén to Tierra del Fuego and Isla de los Estados. To date, no cases of overlap between these two *Pinguicula* species have been reported. Knowing the distribution of species is a key component to understanding their ecology and conservation. The study of the carnivorous plants of Argentina contributes to increase the knowledge of the native flora.

Introduction

The *Pinguicula* species of Argentina are perennial herbs that grow as rosettes attached to the ground that rarely exceed 3.5 cm in diameter. The upper side of the leaves are covered with glands that produce a mucilaginous secretion. Small insects get stuck in the mucilage and are degraded by enzymes secreted by the referred glands. The absorbed nutrients are important sources of nitrogen for these plants (Dawson 1973). In autumn-winter they spend several months under the snow with the same type of leaves, being homophilic species, unlike others in the genus. In summer they develop one or more inflorescences consisting of a single flower through which they reproduce sexually. At first glance the two species appear similar, but if different characters of the inflorescence are punctually compared, the morphological distinction is achieved. These two *Pinguicula* grow in the Andean Patagonian Forest ("*Bosque Andino Patagónico*") ecoregion, but in very different environments. The habitat of *P. antarctica* corresponds to the peat bogs of the Patagonian rainforest (temperate rainforest) with reported sightings in Chubut, Santa Cruz, Tierra del Fuego, and Isla de los Estados (Dawson 1973). The plants occur from sea level to elevations of approximately 1000 m above sea level. The associated floristic set is Subantarctic (Lampard *et al*. 2016).

Pinguicula australandina has been determined to occur at elevations of 1400 to 2300 m above sea level, mainly in alpine pastures between 36° and 41° South latitude both for Argentina and Chile, in the former the reported sightings place populations in Neuquén and Río Negro (Lampard *et al*. 2016). A particularly interesting population of *P. australandina* has been sighted in a specific location in Puerto Blest (Río Negro) (Figs. 1 & 2), a habitat similar to the description of the ecosystem preferred by *P. antarctica*, growing on sphagnum peat moss and close to 790 m above sea level (Brion *et al*. 1988).

Methodology

In January 2020, within the framework of the "Carnívoras Argentina" project, an investigation was carried out in the Nahuel Huapi National Park in order to compare distinct populations of *P.*

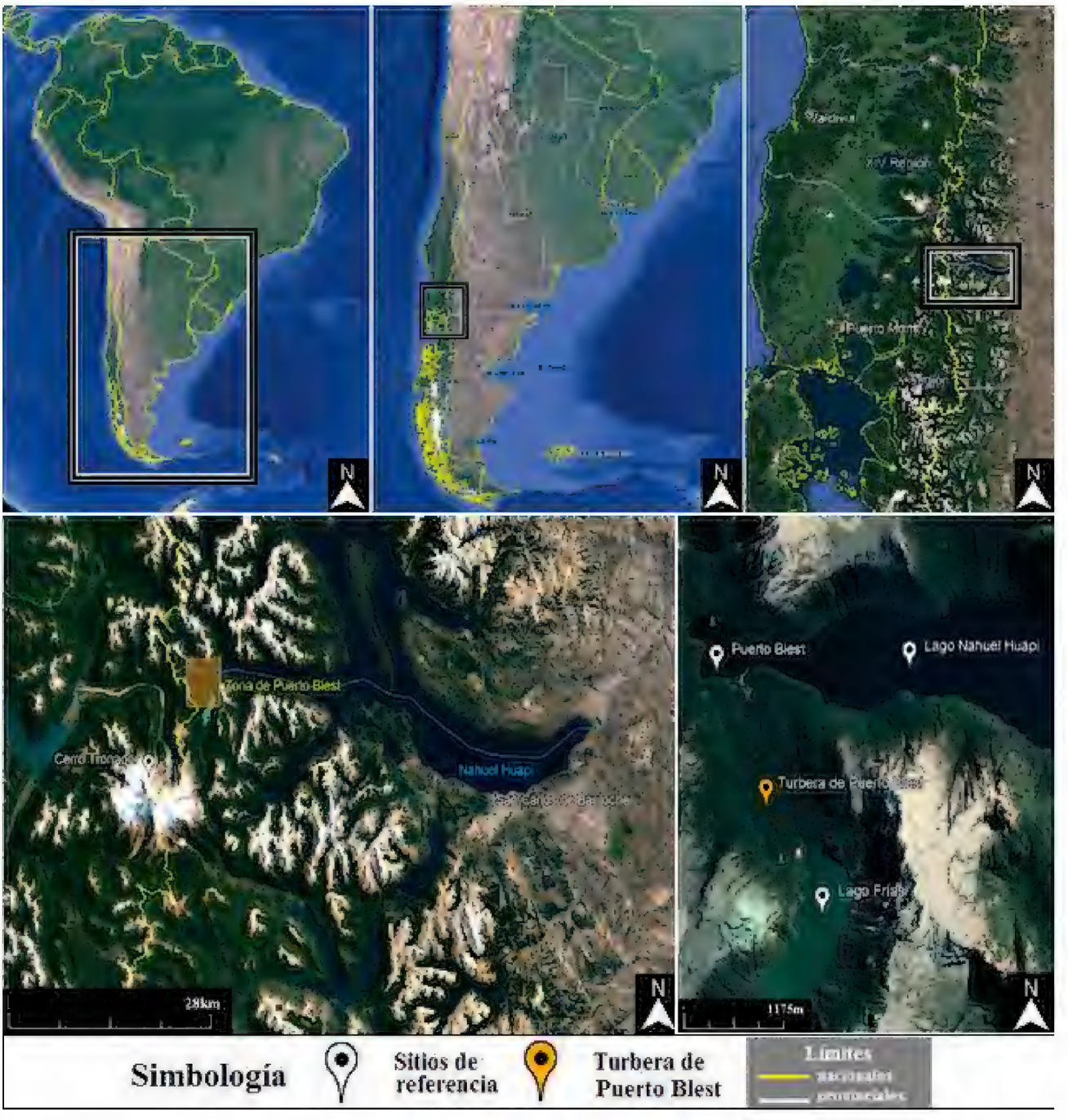


Figure 1: Location of the Puerto Blest peat bog. Satellite images taken from Google Earth. Image date according to satellite data: 10/17/2019.

australandina that exhibited morphological differences in their native habitat and determine if these differences prevailed in *ex-situ* cultivation (under the same growing conditions). Three previously known locations were surveyed, two of which were located in hills near the City of San Carlos de Bariloche over 1600 m above sea level, in high Andean pastures. The other location corresponds to the peat bog present in the Puerto Blest area. In this publication we will refer exclusively to the findings at this location. The survey method was *in-situ* photography, making measurements of the plants and recording the captures of invertebrates with macro photos. At the same time, with the permission of the National Parks Administration (Research Authorization - DRPN - No. 1676), live material was collected. With the collected material, two herbarium specimens were prepared.

With the photographic material generated *in-situ* and the collection of specimens, we proceed to review the specific bibliography with botanical description of the *Pinguicula* known in Argentina

Figure 2: Puerto Blest peat bog at 790 m above sea level. Photo taken 01/07/2020.

using the most recent works on the genus, viz. *Pinguicula* of Latin America, Vol. 2 (Lampard *et al*. 2016) and the review Revision of *Pinguicula* (Lentibulariaceae) in Chile and Argentina (Gluch 2017a,b).

In Puerto Blest, the meteorological, soil, and consequently ecosystem characteristics differ greatly from other sectors of the Nahuel Huapi National Park, giving rise to the Valdivian Forest.

Results

The presence of *P. australandina* in Puerto Blest is at least a strange fact, considering the floristic composition and the environment where the other known populations grow in the Cerros de Río Negro in the Nahuel Huapi National Park (Roccia 2018). Despite these environmental differences, the *P. australandina* population from Puerto Blest did not present great differences with the other populations observed (beyond those differences in color, typical of the varying light conditions) (Fig. 3). However, it was noted that the *P. australandina* population in Puerto Blest was more advanced in terms of fruit and seed development, possibly due to being approximately 790 m above sea level,

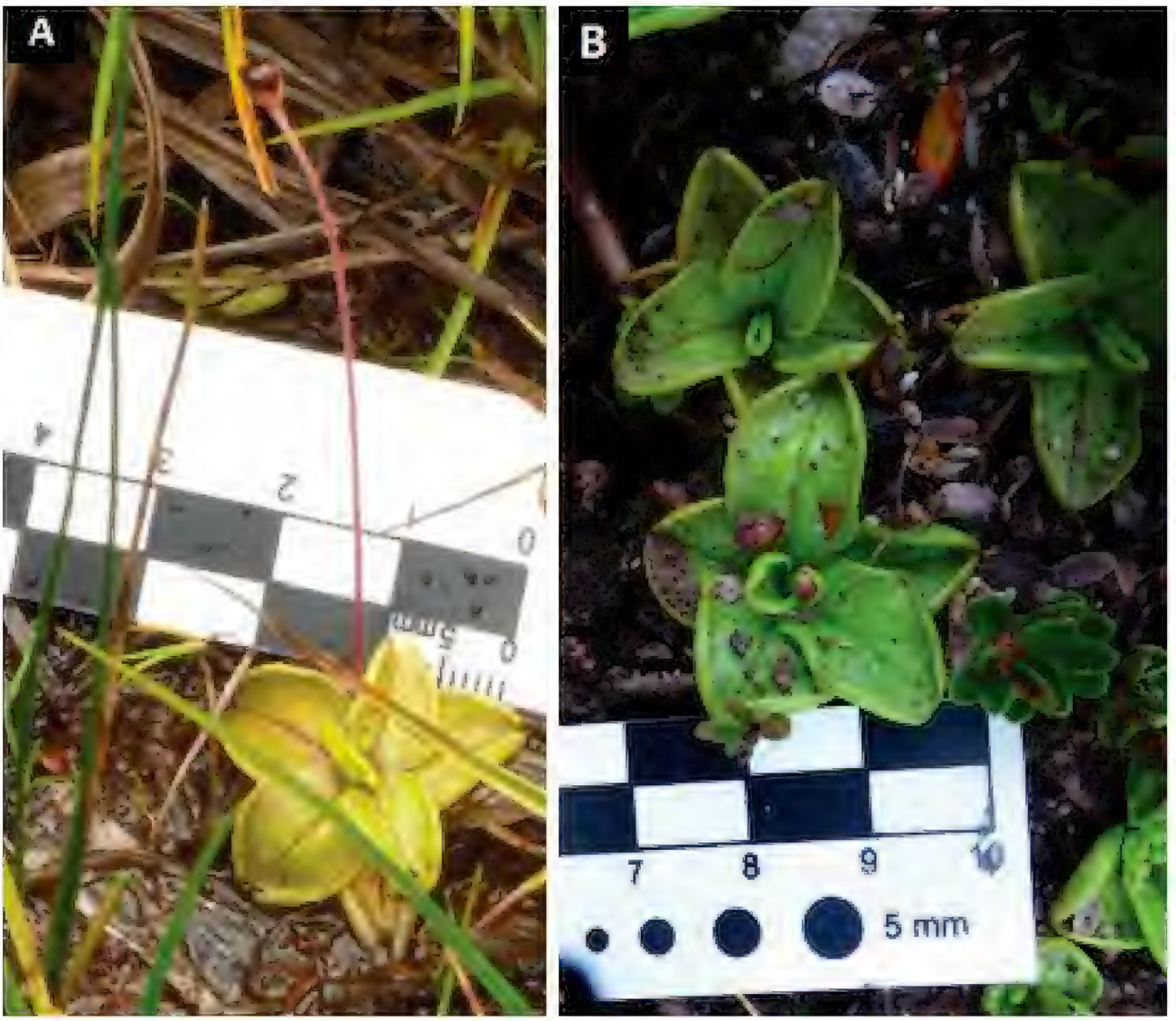


Figure 3: (A) *Pinguicula australandina* in Puerto Blest. Photo taken 01/07/2020. (B) Same species in a meltwater stream at 1600 m above sea level on a hill near San Carlos de Bariloche. Photo taken 01/05/2020.

while the populations that were above 1600 m above sea level were in a less developed flowering stage at the same time of the year (personal observations making comparisons in the flowering stages in an altitude gradient for the same hill).

In the survey and detailed observation in different sectors of the peat bog, where access was only possible thanks to the explicit permission of the Administration of National Parks within the framework of the proposed investigation (DRPN - N° 1676), *Pinguicula* with very different morphology were found, with widely involute leaves and longer floral scapes (Fig. 4).

Discussion

When carrying out the morphological comparison between the different Puerto Blest specimens, we consider the possibility that the *Pinguicula* with very involute leaves corresponds to *Pinguicula antarctica*.

P. antarctica and *P. australandina* are species that can appear to be very similar. Faced with different environmental conditions, the leaves can be more or less involute and their colors can vary from yellowish green to reddish (personal observations). These differences even occur in the same species

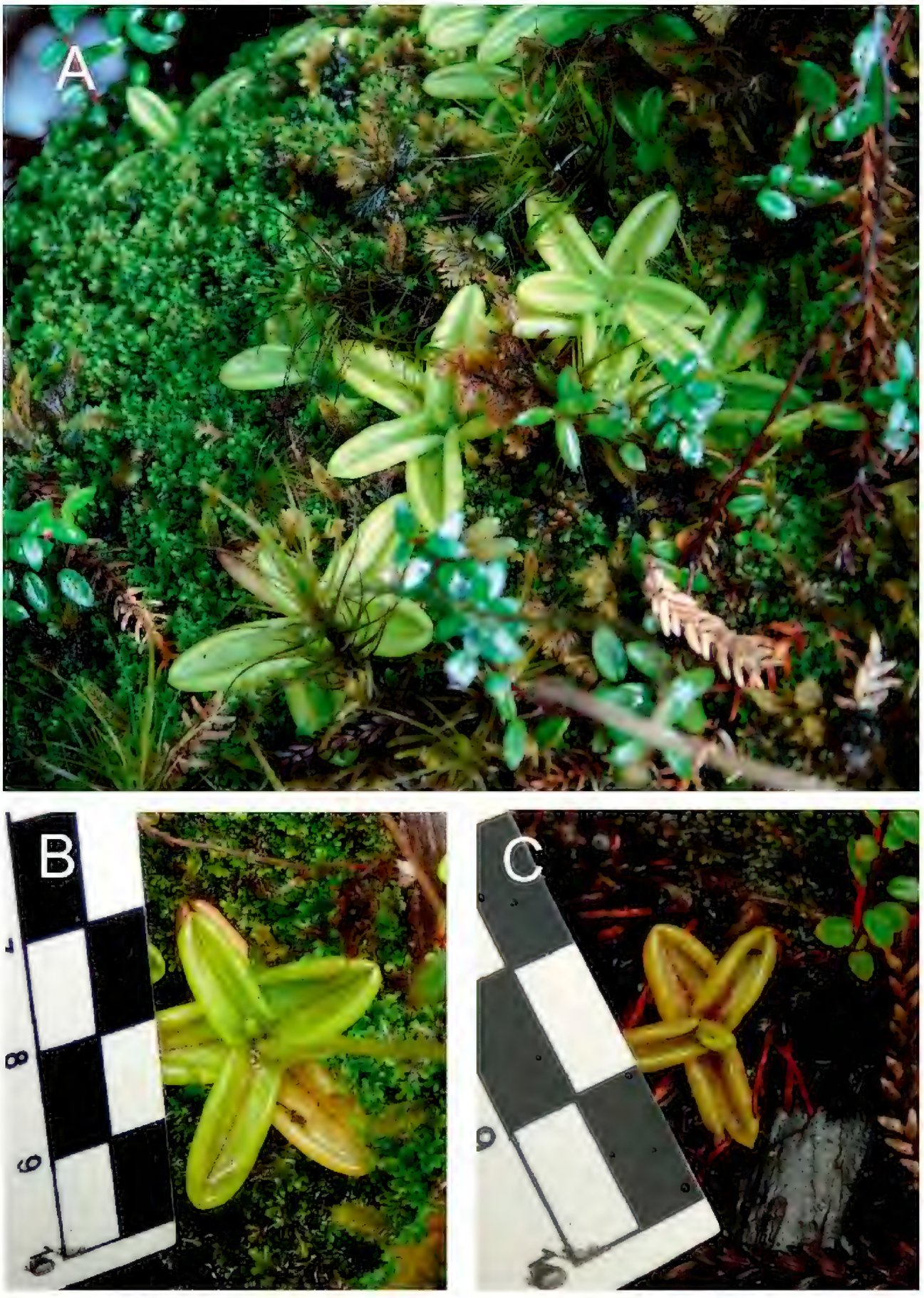


Figure 4: Several specimens of the *Pinguicula* with very involute leaves in Puerto Blest. (A) Group growing on moss and logs. (B) Adult specimen with developed floral scape. (C) Smallest specimen. Photos taken on 01/07/2020

Table 1. Adaptation of Gluch 2017a,b. * White corolla *P. australandina* has been observed. ** Differences in fruit shape were described by Gluch in personal communications.

Comparison reference	Organ	*P. australandina*	*P. antarctica*
#1	Length of floral scape	2-5 cm long.	4.5-20 cm long.
#2	Spur	2-3 mm conical and with pointed end. Solid green or yellow.	1-1.5 mm. shaped like a sack. With parallel violet lines.
#3	Corolla's shape	Sub-isolobada. The 2 petals of the upper lip are sub-equal to the 3 of the lower lip.	Bilaviated. The 2 petals on the upper lip are considerably shorter than the 3 on the lower lip, almost half.
#4	Presence of glands in floral scape	The entire scape moderately covered with glandular hairs.	Almost glabrous in the upper part of the stem, the presence of glandular hairs increases towards the base.
#5	Corolla's color	Pink, white*, lilac or purple	White
#6	Palate's location	Below the middle lobe inside the tube	At the base of the middle lobe of the lower lip.
#7	Fruit shape**	Globular or ovoid.	Elongated, slightly cylindrical, with a flat edge

under different environmental conditions (Aranoa 2018) which could lead to confusion. However, the differences that ensure the determination for these species are found in the floral organs.

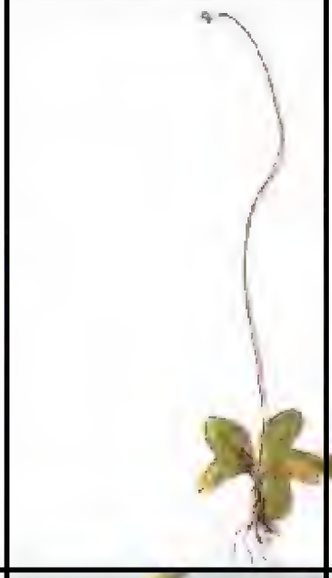
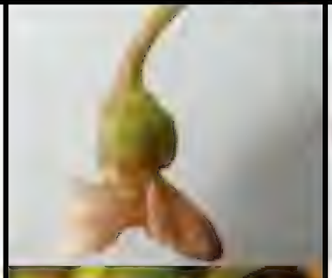
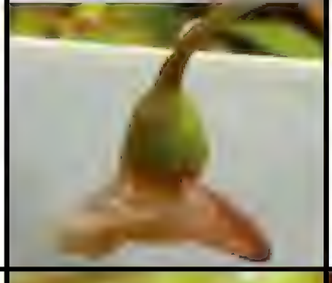
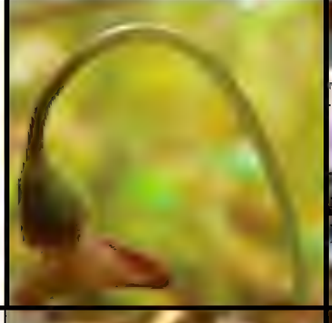
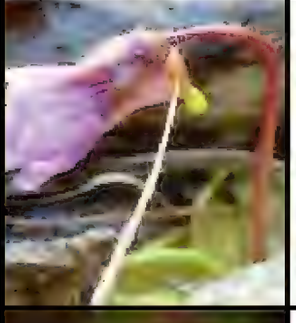
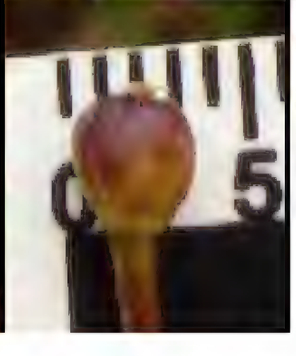
In addition to the morphological differences compared in Table 2, photos provided by the Puerto Blest tourist guides were reviewed to complement this comparative analysis. In this photographic review, a flower of *P. antarctica* is found in good condition in that locality (Fig. 5), thus confirming the presence of both species in the same location.

In consultation with other specialists of the genus *Pinguicula* from Latin America (Fernando Rivadavia and Oliver Gluch), the question was raised about another record of overlap between these two *Pinguicula* species. In Rodriguez *et al.* (2008) both species were recorded, but *P. australandina* in the Baker River Basin and *P. antarctica* in the Pascua River Basin, in Chile. Both basins have marked differences in location (Sandoval *et al.* 2016), not being a registered case of habitat overlap.

Conclusion

In January 2020, *P. antarctica* was found in the Puerto Blest bog. This is the most northern record for this species in Argentina, expanding its known distribution to Tierra del Fuego and Isla de los Estados, Santa Cruz, Chubut, and Río Negro. At the same time, in the present study, *P. antarctica* and *P. australandina* were found in an area of less than 400 m^2 in the Puerto Blest bog (Fig. 6), being the first record of an overlap between *P. antarctica* and *P. australandina*.

Table 2. Visual comparison between the floral characters of the Pinguiculas. All photos correspond to the Puerto Blest peat bog, except for #2 Spur and #4 Presence of glands in floral scape on *P. australandina* (# refers to Table 1).

Comparison reference	*P.antarctica*	*P.australandina*	Discussion
#1 Length of floral scape			*P.australandina* exhibits a scape between 2-5cm long (8). *P.antarctica*´s can greatly exceed this length, as evidenced by photographs and herbal material. On-site photos taken in Puerto Blest on 01/07/2020.
#2 Spur	 		The inflorescences found were in an advanced flowering stage.The spur´s sack-shape is clear in *P.antarctica*, even when comparing with an old corolla of *P.australandina* which keeps its sharp conical shape.
#4 Presence of glands in floral scape			*P.australandina* is moderately covered with glandular hairs in the top of scape, but *P.antarctica* is almost glabrous.
#7 Fruit shape			The fruits of the two species are slightly different.

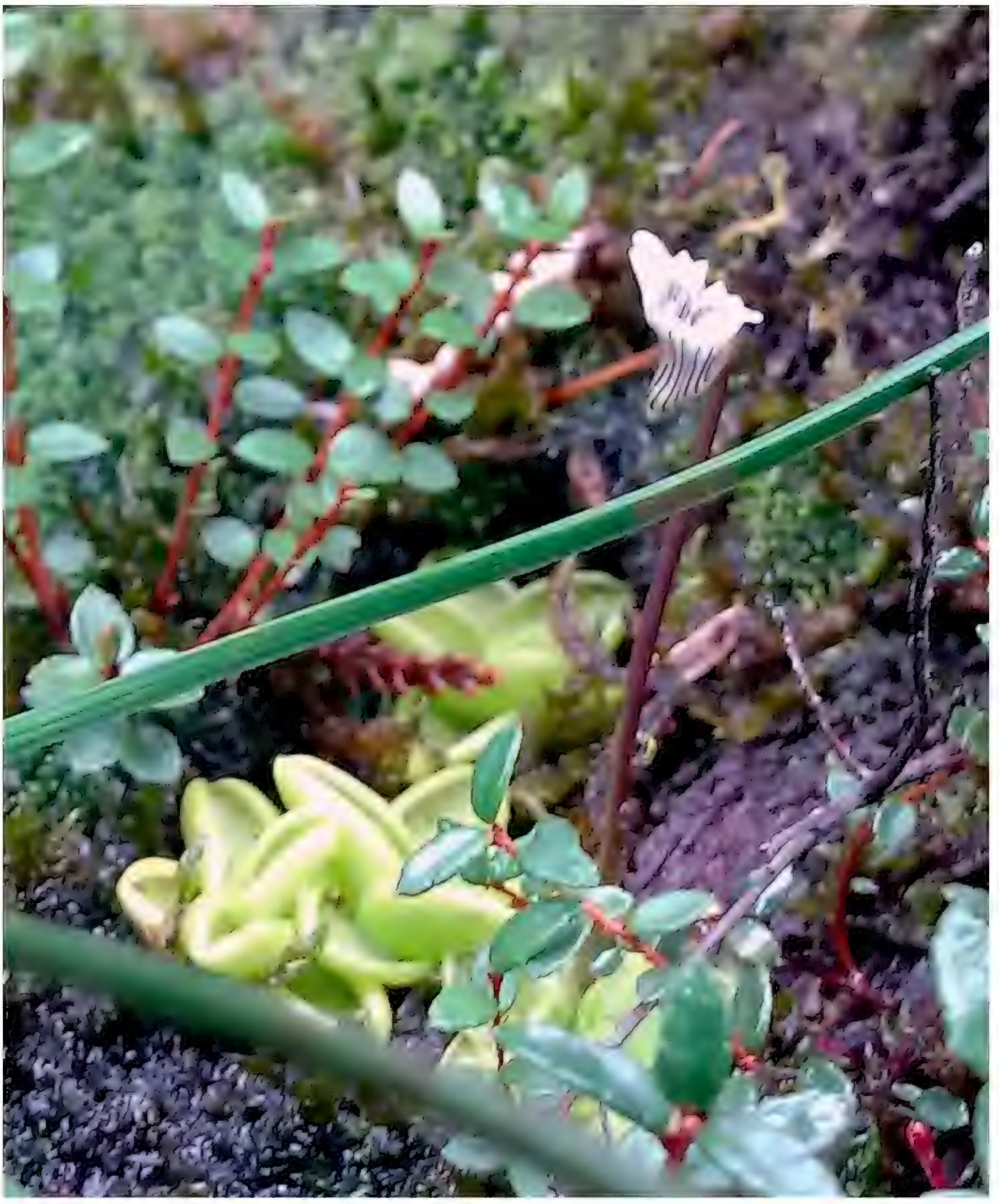


Figure 5: *Pinguicula antarctica* in flower in the bog of Puerto Blest. Maria Fernanda Tazzin.

Acknowledgements: To Fernanda Tazzin and her lovely family, for helping us so much. Without their support, this research would not have been possible.
To Nadia Valeria Velázquez Barloa, for the time she spent helping us with the presentation of the research project.
To Cecilia Núñez, from the North Patagonia Regional Office, and Susana Seijas, from the Nahuel Huapi National Park, for trusting us and having stimulated the investigation.
To Danel Josu Aranoa, Belén Arce, Ignacio, and Juan Merino Mancioli, for having collaborated with the locations to understand more about the Pinguiculas of the Nahuel Huapi NP.

Figure 6: Spatial distribution of *P. antarctica* and *P. australandina* found in the study area.

To Patricio Gregoris, for his photo of *P. antarctica* and all the information shared about the native carnivorous flora of Patagonia.
To Sandra Mantoani, for her insistent actions over time to make dreams come true.
To Mariano Rubén Saviello, for encouraging the spirit of the publication.
To Fernando Rivadavia and Oliver Gluch, for their contributions to this publication.
To Manuel Zurbano, for the English translation of this research.

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Additional features for the recently described *Pinguicula* (Lentibulariaceae) species from Spain

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Keywords: *Pinguicula casperiana*, Lentibulariaeae, Serranía de Cuenca, Spain.

Abstract: Two new butterwort species, *Pinguicula casperiana* and *P. tejedensis*, from Central Spain have been recently described, and the name *P. submediterranea* has been resurrected in the same publication. My article describing "*P. conquensis*" was under review at that time and this plant is exactly the same as *P. casperiana*. As it gives additional morphological diagnostic characters, it is worth bringing it to everyone's attention for a better understanding of this species. Additional comments are made about *P. submediterranea* and *P. tejedensis* as those populations were also studied in my article: those names are here considered later synonyms of *P. dertosensis*. *Pinguicula casperiana* raises to eleven the number of *Pinguicula* species from Spain, being the sixth endemic to the Iberian Peninsula.

Introduction

With approximately 360 species, Lentibulariaceae Rich. is the most diverse family of carnivorous plants (Fleischmann & Roccia 2018). Among these, the genus *Pinguicula* L. accounts for ca. 105 species (Juárez-Gutiérrez *et al.* 2018; Casper 2019; Zamudio & Vega 2019; Zamudio *et al.* 2019; Casper *et al.* 2020). Mexico and the Mediterranean basin represent the two main diversity centers of the genus (Fleischmann & Roccia 2018).

The last revision of the *Pinguicula* species in Spain and Portugal (Blanca *et al.* 1999) and the Flora Iberica (Blanca 2001) list nine species in the Iberian Peninsula: *P. alpina* L., *P. dertosensis* (Cañig.) Mateo & M. B. Crespo, *P. grandiflora* Lam., *P. longifolia* Ramon ex DC., *P. lusitanica* L., *P. mundi* Blanca, Jamilena, Ruíz-Rejón & Reg. Zamora, *P. nevadensis* (Lindb.) Casper, *P. vallisneriifolia* Webb, and *P. vulgaris* L. A tenth new species was added in 2018, *P. saetabensis* M. B. Crespo, Mart.-Azorín & M. A. Alonso (Crespo *et al.* 2018). Populations from central Spain have been a matter of debate: they were treated as belonging to *P. mundi* (Blanca *et al.* 1999; Blanca 2001) or to *P. dertosensis* (Roccia *et al.* 2016), or as "morphologically distinct" (Crespo *et al.* 2018).

While reviewing herbarium material, pictures from botanical fieldtrip to this region, and cultivated material, it became clear that these populations represent a new species, planned to be named "*Pinguicula conquensis*". The article has been submitted to a peer-reviewed journal and it was only a matter of days before it should have been published. However, in the meantime, another article was realised describing two new species, *P. casperiana* and *P. tejedensis*, and resurrecting the name *P. submediterranea* (Crespo *et al.* 2020). "*Pinguicula conquensis*" and *P. casperiana* are in fact one and the same species and my article got rightly rejected for that reason. Nonetheless, it is worth adding the taxonomical features forecast in my article to the ones of Crespo *et al.* (2020) for a better understanding of this species.

Material & methods

Morphological analysis for the description of the new species is based on field observations during a fieldtrip to Spain in 2010, on examination of cultivated material, herbarium specimens held at

ALBA, BC, GADC, JACA, MA, MAF, and P (Thiers 2019) and *in situ* photographs of independent observers. The distribution map was drawn based on all those records using QGIS software in its 3.12.1 version. Conservation status is discussed following the IUCN (2012) Red List categories and criteria.

Results

Below is the description of "*Pinguicula conquensis*" as it was submitted to the peer-reviewed journal:

Diagnosis

Pinguicula casperiana is morphologically close to *P. dertosensis* and *P. mundi*. It differs from *P. dertosensis* by i) its divergent corolla lower lip lobes (vs. overlapping in *P. dertosensis*), ii) its calyx lower lip lobes fused on ½ or more of their length (vs. free to fused on less than ½ of their length in *P. dertosensis*), iii) the flat to slightly involute margin of its spring leaves (vs. involute margins in *P. dertosensis*), iv) its ovoid capsules with pointed tip (vs. rounded without prominent tip in *P. dertosensis*), and v) its bigger (0.65-0.8 mm long) and more rectangular seeds with micropylar appendage (vs. smaller (0.5-0.6 mm long) and subglobose to ovoid seeds without micropylar appendage in *P. dertosensis*) (Fig. 2). It differs from *P. mundi* by i) having ovoid capsules with pointed tip (vs. rounded to subglobose in *P. mundi*), ii) its shorter spur, about ⅓ of the whole corolla length (vs. about ½ in *P. mundi*), iii) its acute triangular calyx lobes (vs. rounded to subobtuse elliptic calyx lobes in *P. mundi*), iv) its shorter (up to 7(-12) cm long) summer leaves (vs. up to 18.5 cm long in *P. mundi*) and v) its smaller (0.65-0.8 mm long) seeds with micropylar appendage (vs. bigger (0.8-1.0 mm long) seeds without micropylar appendage in *P. mundi*) (Fig. 4). Additionally, the three species occur in distinct geographic areas (Fig. 3).

Etymology

Pinguicula casperiana was planned to be named "*P. conquensis*" after the Serranía de Cuenca, where it occurs. "*conquensis*" is an adjective referring to the town of Cuenca, that gives its name to the Serranía de Cuenca. "*casperiana*" is a tribute to S. Jost Casper.

Type material planned for "*Pinguicula conquensis*"

SPAIN • Cuenca, Beteta, Hoz de Beteta; 30TWK79; 1100 m; 09 Jun. [19]89; *Gamarra, Garilleti & F. Lara s. n.*; holotype: MA[MA-01-00472045] photo !; isotype: MA[MA-02-00472045] photo !.

Description (Fig. 1–3)

Small perennial *herb* with slender white roots, overwintering as a hibernaculum. *Leaves* arranged in a rosette emerging from the ground; spring leaves (before anthesis) (4-)5-8 in number, yellow-greenish, sometimes tinged with red, adpressed on the ground, shortly petiolate, oblong-elliptic, abaxially glabrous, adaxially densely covered with short stipitate and sessile glands, with flat to slightly involute margins and a rounded apex, 2.5-3.6 cm long and 1.1-1.8 cm wide; summer leaves (after anthesis) different from spring leaves, (3-)4-6(-8) in number, yellow-greenish, sometimes tinged with red, semi erected, shortly petiolate, obovate, abaxially glabrous, adaxially densely covered with short stipitate and sessile glands, with revolute margins and a rounded apex, 4.5 6.9(-11.9) cm long and 1.6-2.0(-2.5) cm wide. *Flower scapes* 1-3(-4), 6.9-7.5 cm long, terete, 1-flowered, yellow-greenish and sparsely glandular at the base, red-violet and densely glandular near the flower.

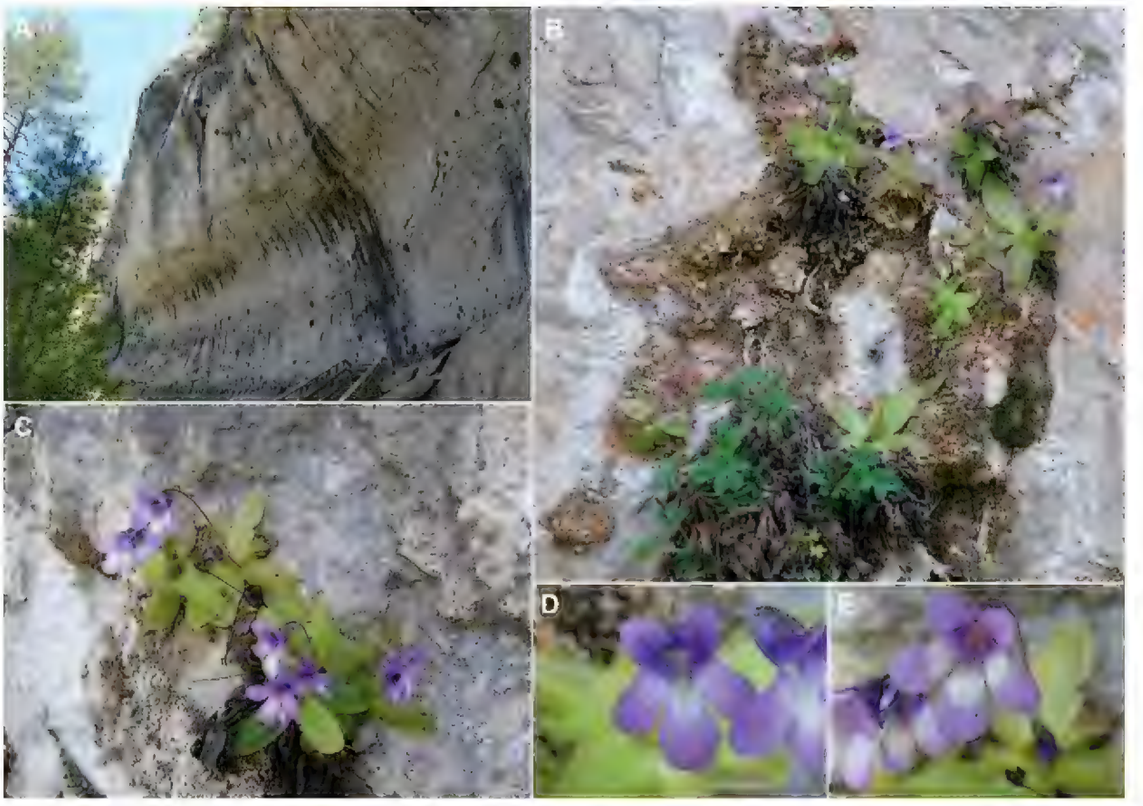

Figure 1: *Pinguicula casperiana* M.B.Crespo, Mart.-Azorín, M.Á.Alonso & L.Sáez at the Huelga de Don Juan location. A: vertical limestone cliffs, typical habitat for this species. B: plants growing in a thin layer of tufa concretion and moss, associated with *Potentilla caulescens* L. C: habit. D, E: front views of two flowers, showing variation.

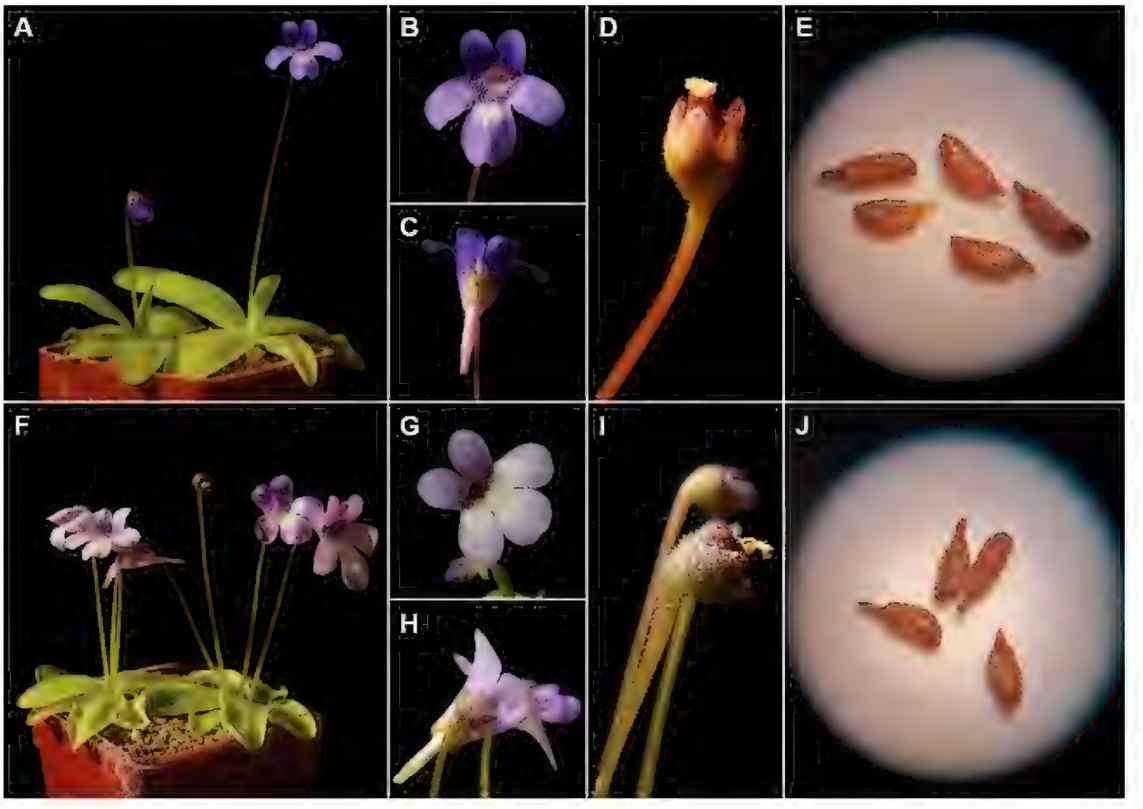

Figure 2: Comparison between *Pinguicula casperiana* M.B.Crespo, Mart.-Azorín, M.Á.Alonso & L.Sáez (A-E) and *P. dertosensis* (Cañig.) Mateo & M. B. Crespo (F-J). A, F: habit. B, G: front view of the flower. C, H: flower viewed from above. D, I: seedpod. E, J: seeds (same magnification (X20) was used for both pictures).

Figure 3: Distribution map of the three species treated in this study: white dot, *Pinguicula casperiana* M.B.Crespo, Mart.-Azorín, M.Á.Alonso & L.Sáez; grey dot, *P. dertosensis* (Cañig.) Mateo & M. B. Crespo; black dot, *P. mundi* Blanca, Jamilena, Ruíz-Rejón & Reg. Zamora. Stars indicate the type locations of each species.

Figure 4: *Pinguicula mundi* Blanca, Jamilena, Ruíz-Rejón & Reg. Zamora at its type location, for comparison with *P. casperiana* M.B.Crespo, Mart.-Azorín, M.Á.Alonso & L.Sáez (Figs. 1 & 2). A: habit. B: three quarter view of the flower showing the long spur. C: seedpods. D: flowering plant showing the first elongated summer leaves. E: plant at the end of the growing season, showing the typical elongated summer leaves. C from Oliver Gluch, all others from the author.

Calyx bilabiate, 5-lobed, violet, densely covered with stipitate glands, persistent during fructification; 3 upper lip lobes triangular-ovate, with an acute to subacute apex, 3.0-4.0 mm long, 1.0-1.5 (-2.0) mm wide, divided to near the base; 2 lower lip lobes ovate, with an acute to subacute apex, 3.0-4.5 mm long, (1.0-)1.5-2.0 mm wide, united from the base on *c.* ½ of their length, subparallel to slightly divergent. *Corolla* bilabiate, 5-lobed, 20-30 mm long (spur included), blue-violet in its overall, with a 90-110° opening angle; 2 upper lip lobes blue-violet, sometimes marked with a dark blue-violet vein at the base, oblong, with a rounded apex, 4.0-5.5(-7.5) mm long, 3.0-4.5(-7.0) mm wide; 3 lower lip lobes blue-violet on the distal part, white on the proximal part (sometimes the lateral lobes completely blue-violet) and sometimes marked with dark blue-violet veins near the throat, bearing *c.* 0.75 mm long white clavate hairs on the proximal part, the lateral ones oblong-obovate with a rounded apex, longer than wide, 5.0-8.0(-10.0) mm long, 4.0-7.5 mm wide, the middle one larger than the lateral ones, obovate with a rounded apex, sometimes with a yellow spot at the very base, 7.5-11.0 mm long, 6.0-9.0(-11.0) mm wide, divergent, not overlapping, with non-waving margins. *Throat* totally dark violet, except a thin whitish band on top of the middle lobe of the lower corolla lip, bearing *c.* 0.75 mm long white clavate hairs. *Tube* medium-sized, 5.5-8.5(-11.5) mm long, (4.0-)6.0-8.5(-10.5) mm wide, broadly funnel-shaped, blue-violet near the corolla lobes, violet tinged with red near the spur and whitish with dark violet veins on the lower side, sparsely covered by stipitate glands on the outer side. *Spur* blue-violet to red-violet, medium-sized, 5.5-7.0(-9.5) mm long, subulate, straight to slightly curved downwards, with an acute and sometimes slightly bifid apex, sparsely covered by stipitate glands on the outer side. *Stamens* 2, *c.* 2 mm long; filaments *c.* 1.5 mm long, white, curved, surrounding the ovary; anthers *c.* 0.5 mm long, light yellow, +/- confluent, roofed by the stigma lower lip lobe. *Pollen* light yellow, aperture not studied. *Ovary* pale green, subglobose, sessile, covered by short stipitate glands, *c.* 1.5 mm in diameter, 2-carpellate, 1-loculate, ending in a short style; central placentation free, with numerous free sessile ovules. *Stigma* white tinged with violet, short, 2-lobed, with crested upper surfaces, persistent on the fruit; the lower lobe ovale, *c.* 2 mm wide, fringed; the upper lobe much smaller, narrowly triangular, *c.* 0.75 mm long, not fringed. *Capsule* yellow-greenish at the base, usually tinged with red mostly near the tip, ovoid with acute tip, 3.0-4.5 mm long and 2.0-2.6 mm large, sparsely covered by short stipitate glands; maroon when mature and then dehiscent. *Seeds* brown, elliptic to oblong, 650-800 µm long, 230-300 µm thick, stipitate with a 110-135 µm long funicle, outer coat reticulate with subrounded to ovale interspaces, with a single very short micropylar appendage (10-30 µm long). *Chromosome number* 2n = 64 (Casper & Stimper 2009).

Phenology

Pinguicula casperiana starts flowering in April and can flower up to June.

Habitat and ecology

Pinguicula casperiana is typically found on vertical limestone cliffs, in deep humid gorges, at an altitude of 860-1220 m a.s.l. Plants are growing in a thin layer of tufa concretion and moss, accumulating in rock crevasses where water seeps from the cliff. It is usually growing alone but can shares such habitat mainly with *Potentilla caulescens* L., and sometimes with *Adiantum capillus-veneris* L. (Fig. 1).

Distribution

Pinguicula casperiana is endemic to the Serranía de Cuenca, in central Spain. Most populations occur in the Cuenca province, and a few locations are also known in the Guadalajara province

(Fig. 3). Up to now, no reference to its presence in the nearby Teruel province have been found, but it has to be searched in the east of this province.

It has been observed a morphological gradient for *Pinguicula casperiana* leaf along its distribution range: to the north, summer leaves are different from spring leaves (anisophyllous), being longer and with revolute margins, while towards south, they tend to be rather identical to spring leaves (heterophyllous), being shorter and with involute margins.

Conservation status

It was not possible to investigate the number of plants in each known location in the timeframe of this study, so that *Pinguicula casperiana* should be classified at DD (data deficient) (IUCN 2012). However, comparing photographs of the same sites (Huelga de Don Juan and Hoz de Priego) taken several years apart, it is obvious that the number of plants decreases as the cliffs are becoming drier. The vulnerability of *Pinguicula casperiana* has thus to be further investigated.

Additional specimens examined

Pinguicula casperiana:

Herbarium vouchers:

SPAIN - **Cuenca** • Beteta, Cañon del Tajo, Estrecho del Horcajo; 30TWK874959; 1130 m.; paredones calizos hacia el W.; 08 Aug. 1997; *L. M. Ferrero, L. Medina LM726*; MA[MA-01-00594441] photo! • Fuerte-Escusa, hacia Poyatos, balma al pie del rio Escalvas; (30T WK77); 23 Jun. 1983; *Benedí, Blanché, Molero & Vallès s. n.*; BC[BC-652886] photo! • Ib., 23 Jun. 1983; *Benedí, Blanché, Molero & Vallès s. n.*; MA[MA-01-00334328] photo! • Ib.; 23 Jun. 1983; *Benedí, Blanché, Molero & Vallès s. n.*; MAF[122615] photo! • Hoz de Beteta; En los muros rocosos humedos calizos; 11 Jul. 1932; *Prof. A. Caballero s. n.*; MA[MA-01-00115271] photo! • Ib.; común en las fuentes y sitios húmedos; 11 Apr. 1933; *Prof. A. Caballero s. n.*; MA[MA-01-00115276] photo! • Hoz de Beteta, fuete de los Frenos; 30TWK79; ad 1100 m; in humidis calcareis; 02 Aug. 1975; *Fernández Casas & García Guardia 761*; MA[MA-01-00394319] photo! • Ib.; 02 Aug. 1975; *Fernández Casas & García Guardia 761*; MA[MA-02-00394319] photo! • Ib.; 02 Aug. 1975; *Fernández Casas & García Guardia 761*; MA[MA-01-00439461] photo! • Hoz de Tragavivos; 30T WK78; 990m; calizas liasicas; 26 Jul. 1978; *G. López 773bis GF*; MA[MA-01-00439051] photo! • Huerta del M., Collado Bajo; 01 Jul. 2017; *José Fajardo & Alonso Verde s. n.*; ALBA[10746] photo! - **Guadalajara** • Peralejos de las Truchas, paredones calizos hacia el SW sobre la pista del Tajo; 30TWK868976; 1120m.; 08 Aug. 1997; *L. M. Ferrero y L. Medina LM727*; MA[MA-01-00594442] photo! • Poveda de la Sierra, barranco del Horcajo; 30 0587158 4495363, DATUM SPWGS84; 1250 m; paredones calizos rezumantes; 02 Jun. 2012; *C. Aedo, L.M. Ferrero, J. García & L. Medina LM6270*; MA[MA-01-00867494] photo!.

Populations visited by the author:

SPAIN - **Cuenca** • Beteta, Fuente de los Tilos; 1100 m; 18 May 2010; Aymeric Roccia' pers. observ. • Beteta, Huelga de Don Juan; 18 May 2010; Aymeric Roccia's pers. observ. • Beteta, paredes frente a la Fuente de los Tilos; 1100 m; 18 May 2010; Aymeric Roccia's pers. observ. • Fuertescusa, Cueva del Aire; 977 m; 18 May 2010; Aymeric Roccia's pers. observ. • Priego, Hoz de Priego, site 1; 18 May 2010; Aymeric Roccia's pers. observ. • Ib., site 2; 18 May 2010; Aymeric Roccia's pers. observ.

Photographs examined:

SPAIN - • Sierra de Cuenca; 02 May 2010; Jean-Marc Moingeon's pers. observ. - **Cuenca** • 15 Jun. 2018; Victor Mol's pers. observ. • Beteta, Fuente de los Tilos; Aug. 2018; Eric Partrat's & Laurent Legendre's pers. observ. • Beteta, Huelga de Don Juan; Aug. 2018; Eric Partrat's & Laurent Legen-

dre's pers. observ. • Hoz de Beteta; 1200 m; Apr. 2004; Eric Partrat's, Jean-Rémi Fiéfort's & Serge Lavayssière's pers. observ. • Palomera, Molinos de Papel; Aug. 2018; Eric Partrat's & Laurent Legendre's pers. observ. • Priego, Hoz de Priego; Aug. 2018; Eric Partrat's & Laurent Legendre's pers. observ. • Uña, Rincón de Uña; Aug. 2018; Eric Partrat's & Laurent Legendre's pers. observ.

Pinguicula dertosensis:
Herbarium vouchers:
SPAIN - • Massis del Ports, vers el Barranc de la Guimerana, limit termes de LA SÉNIA (Montsià) i BESEIT (Matarranya); 31T BF61; 820 m; 03 Aug. 1967 ; *L. de Torres s. n.*; BC[BC-905331] photo ! – **Jaén** • Cazorla: barranco de Valdecazores; 30SWG1499; 1460 m; 30 May 1976; *González Rebollar, Muñoz Garmendia & Soriano 3833*; MA[MA-01-00479890] photo! • Cazorla : barranco del Guadalentín; 30SWG1495; 1300 m; ribera; 25 May 1975, *González Rebollar, Muñoz Garmendia & Soriano 3829*; MA[MA-01-00479893] photo! • Ib., 18 Jun. 1975; *González Rebollar, Muñoz Garmendia & Soriano 3830*; MA[MA-01-00479892] photo! • Ib.; 25 Sep. 1975; *González Rebollar, Muñoz Garmendia & Soriano 3831*; MA[MA-01-00479891] photo! • Sierra de Cabrilla; rochers humides et exposés au soleil, sur le calcaire; Jun. 1906; *Elisée Reverchon 1429*; P[P02982059] photo! • Ib.; Jun. 1906; *Elisée Reverchon 1429*; P[P02982060] photo! - **Tarragona** • Pista de Fredes al Monte Caro, barranco de Rafalgari; 40°44′54″N-0°12′53″E, 30TBF6414; 1020 m; 08 Jun. 1999; *C. Aedo, I. Aizpuru, J. Aldasoro, S. Castroviejo, C. Fabregat, P. Fernández, J. Forcadell, M. García, X. Giraldez, J. Güemes, J. Jiménez, S. López, G. Mateo, F. Muñoz, C. Navarro, J. Ninot, J. Pedrol, A. Prunell, E. Rico, Ll. Sáez, I. Soriano, R. Tavera & M. Velayos CN -2449*; MA[MA-01-00626738] photo! • Ports de Tortosa, Barranc de Salt de Cabrit; 29 Jun. 1917 ; *Font Quer s. n.*; BC[BC-53082] photo! • Ports de Tortosa: La Sénia, Vall de la Fou, Cova del Angels; 600 m; in Adiantium, rup. N.; 18 Jun. 1956 ; J. *Cañigueral, A et O. de Bolós et FO. s. n.*; BC[BC-148968] photo! • Tortosa, Roquetas, barranco de la Caramella; 40°48′17″N 00°23′15″E, datum WGS84; 242 m; matorral xerófilo bajo y cauce de arroyo, substrato calizo; 13 Apr. 2011; *T. Buira, J. Calvo & A. Quintana AQ4365*; MA[MA-01-00837334] photo! - **Teruel** • Beceite, Alto Matarrana; 31TBF6520; 750-800 m; Cantil y parte alta con "Arbutus unedo"; 10 Apr. [19]90; *P. Montserrat s. n.*; JACA[0060390] photo! • Puertos de Beceite, in confinibus Aragoniae et Catal., pr. Font del Teix, in initio Barranc del Parrisal; Apr. 1935; *Bartomeus s. n.* ; holotype: BC[BC-87830] photo!.
Populations visited by the author:
SPAIN - **Tarragona** • Roquetes, Cascada de la Caramella; 13 May 2010; Aymeric Roccia's pers. observ.
Photographs examined:
SPAIN - **Castellón** • Fredes - Rosell, 09 May 2015; Guillem Palomo's pers. observ. • Tinença de Benifassà; *s. d.*; José Quiles' pers. observ. - **Granada** • Los Barrancones; 23 May 2014; Christophe Maerten's pers. observ. •Rio Cebollon entre la Cuerda de los Morros y la Loma del Mono; 03 Jun. 2012; Arielle & Enric Marti's pers. observ. - **Jaén** • Cazorla, Torcales del Lobo; a 1750 m de altitud; 02 May 2014; Alfredo Benavente Navarro's pers. observ. - **Málaga** • Sierra Tejeda, El Robledal; 02 Jul. 2008; Joaquín Ramírez's pers. observ. - **Tarragona** • Caramella Schlucht; 23 Apr. 2004; Oliver Gluch's pers. observ. • Montsià; 13 Apr. 2017; unknown's pers. observ. • Roquetes, Font de Cova Avellanes; Aug. 2018; Eric Partrat's and Laurent Legendre's pers. observ. • Tortosa; 25 Apr. 2013; Jean-Marc Moingeon's pers. observ.

Pinguicula mundi:
Herbarium vouchers:

SPAIN - **Albacete** • Cascades ou *choros* près *Riopar* dans la *Sierra de Segura*; 30 Jun. 1850; *E. Bourgeau 647*; P[P02982056] photo! • Ib.; 30 Jun. 1850; *E. Bourgeau 647*; P[P02982057] photo! • Ib.; 30 Jun. 1850; *E. Bourgeau 647*; P[P02982061] photo! • Ib. ; 30 Jun. 1850; *E. Bourgeau 647*; P[P04443793] photo! • Cueva dde Los Chorros près dde Riopar; alt. 1000m; 03 Jun. 1978 ; *Bernard de Retz 77390*; P[P06889416] photo! • Fábricas de S. Juán. Chorros del Río Mundo.; WH4956; Pared coliza rezumante.; 05 Jul. 1987; *Valdés & Herranz s. n.*; ALBA[5246] photo! • "Los Chorros" Nacimiento del Mundo; 06 Sep. 1950; *S. Rivas Goday & A. Monasterio s. n.*; MAF[33498] photo! • Los Chorros pr. Riopar in Reg. Murc.; in cataratas; 18 Jul. 1923; *Cuatrecasas s. n.*; BC[BC-53051] photo! • Ib.; 18 Jul. 1923; *Cuatrecasas s. n.*; BC[BC-53051_a] photo! • Nacimiento del Mundo en Riopar, Los chorros del Rio Mundo, sub El Calar del Mundo; 10 Jul. 1971; *S. Rivas Goday, Ladero, Valdés, Borja s. n.*; MAF[83307] photo! • Nacimiento del Rio Mundo; 04 Jun. 1959; *Rivas Goday, Delgado y Monsterio s. n.*; MAF[82726] photo! • Nacimiento del Rio Mundo en Riopar; 18 Jul. 1951; *S. Rivas Goday s. n.*; MAF[80015] photo! • pr. Riópar, Sierra del Calar del Mundo, nacimiento del rio Mundo, Cueva de los Chorros; alt. 1200 m; 15 Jun. 1993; *R. Zamora s. n.*; holotype: GDAC[37729] photo! • Riopar, Chorros del Rio Mundo; Taludes rezumantes cerca de una cascada; 15 May 2008; *Alonso Verde s. n.*; ALBA[6860] photo! • Riopar, Cueva de los Chorros; calizas; 28 Jun. 1988; *Aparicio, F. García & Silvestre s. n.*; MA[MA-01-00485659] photo! • Riopar, Los Chorros del Mundo; 30S.WH.49.56; 1200 m; Tobas calizas rezumantes; 19 Jul. [19]86; *Jose M.° Herranz s. n.*; MA[MA-01-00361018] photo! • Sa de Alcaraz. Riópar. Subida a la Cueva de los Chorros (Calar del río Mundo); Comunidades briocormofíticas en taludes rezumantes junto a escorrentías permanentes (Eucladio-Pinguiculetum vallisneriifoliae); 17 Jun. 1982; *D. Sánchez-Mata, P. Cantó, S. Laorga & D. Belmonte s. n.*; MAF[110181] photo! • Sierra de Alcaraz, Calar del Mundo; 30S WH4956; 1150m; Fisuras calizas rezumantes; 20 Jul. 1984; *M. Luceño s. n.*; MA[MA-01-00439052] photo! • Sierra de Alcaraz, loco dicto " Los Chorros"; 30 S WH 4956; ad 1.100m; in scopulis humidis ad cataractam; 28 May 1976; *J. Fernández Casas, J. Fernández Piqueras, M. T. Palomeque et M. E. Sánchez García 1154*; BC[BC-626256] photo! • Ib.; 28 May 1976; *J. Fernández Casas, J. Fernández Piqueras, M. T. Palomeque et M. E. Sánchez García 1154*; MA[MA-01-00208452] photo! • Ib.; 28 May 1976; *J. Fernández Casas, J. Fernández Piqueras, M. T. Palomeque et M. E. Sánchez García 1154*; MA[MA-02-00208452] photo! • Ib.; 28 May 1976; *J. Fernández Casas, J. Fernández Piqueras, M. T. Palomeque et M. E. Sánchez García 1154*; MA[MA-01-00354192] photo! • Ib.; 28 May 1976; *J. Fernández Casas, J. Fernández Piqueras, M. T. Palomeque et M. E. Sánchez García 1154*; MA[MA-01-00421980] photo! • Ib.; 28 May 1976; *J. Fernández Casas, J. Fernández Piqueras, M. T. Palomeque et M. E. Sánchez García 1154*; MAF[150816] photo!.

Populations visited by the author:

SPAIN - **Albacete** • Riópar, Nacimiento del Río Mundo; 12 Aug. 2008; Aymeric Roccia, pers. observ. • Ib.; 14 May 2010; Aymeric Roccia's pers. observ.

Photographs examined:

SPAIN - **Albacete** • Calar del Río Mundo; 2014; Enric Marti's pers. observ. • Cueva de los Chorros; 21 May 2000; Oliver Gluch's pers. observ. • Ib.; 18 Jul. 2004; Oliver Gluch's pers. observ. • Nacimiento del Río Mundo; Aug. 1995; Serge Lavayssière's pers. observ. • Ib.; Apr. 2003; Eric Partrat's pers. observ. • Ib.; 07 May 2010; Jean-Marc Moingeon's pers. observ.

Pinguicula sp.:

Herbarium vouchers:

SPAIN - **Guadalajara** • Checa, turbera junto a la pista del Tajo; 30TXK006745; 1530 m; 25 Jun. 1997; *L. M. Ferrero & L. Medina LM718*; MA[MA-01-00589325] photo!.

Populations visited by the author:

SPAIN - **Cuenca** • Tragacete, Ojuelos de Valdeminguete; 1585 m; 19 May 2010; Aymeric Roccia's pers. observ.

Photographs examined:

SPAIN - **Teruel** • Iglesuela del Cid, barranco de la Tosquilla; 1280 m; ladera caliza umbrosa con bosque mixto; s. d.; Silvia López Udias' pers. observ.

Discussion

Pinguicula casperiana has been treated diversely in the past. In Blanca *et al.* (1999) and the subsequent chapter of Flora Iberica (Blanca 2001), it was considered as northern populations of *P. mundi*. However, as stated above in the diagnosis, it can be morphologically distinguished by leaf, flower, fruit and seed characters (Figs. 2 & 4). Later, Roccia *et al.* (2016) treated these populations as *P. dertosensis*, but *P. casperiana* also differs from this last one by a number of vegetative, floral and reproductive diagnostic characters described in the diagnosis (Fig. 2). Thus *P. casperiana* truly represents a morphologically distinct species in the Iberian Peninsula, further supported by its geographically distinct distribution range (Fig. 3).

Pinguicula casperiana chromosome number was first studied by Casper & Stimper (2009), based on material from the Hoz de Beteta (quoted as *P.* cf. *vulgaris* "Hoz de Beteta"). With 2n = 64, it is an octoploid species and cannot be caryologicaly discriminated from *Pinguicula dertosensis* and *Pinguicula mundi*. Those two were first reported as hexaploid species (Zamora *et al.* 1996), but Casper & Stimper (2009) have not been able to confirm these results. It was then hypothesized that they all three belong to a "*P. vulgaris*-like" group of species from central Spain (Casper & Stimper 2009). However, a recent ITS-based molecular phylogeny study showed that *P. dertosensis* and *P. mundi* are well separated within the phylogenetic tree of European species, belonging to E1a and E3a subclades, respectively (De Castro *et al.* 2016). The recently described *P. saetabensis*, another species from Central Spain, is phylogenetically related to *P. mundi* (Crespo *et al.* 2018). Unfortunately, *P. casperiana* samples were not included in those two studies. Studying DNA material of *P. casperiana* would show if it is more related to *P. dertosensis* or to *P. mundi*.

The exact expansion to the east of *Pinguicula casperiana* has still to be explored. As said before, no population in the Teruel part of the Serranía de Cuenca has been found during fieldtrips, in the herbaria or in the literature. However, some locations exist between the Serranía de Cuenca and the Massís dels Ports and have to be investigated to decipher if they belong either to *P. casperiana*, *P. dertosensis* or another species. For example, the population in Iglesuela del Cid (Teruel province) has been a matter of debate. It was long thought to be *P. dertosensis*, but a recent report discards this possibility and rather assigns it to *P. vulgaris* (López Udias *et al.* 2016). However, such populations have not been visited by the author for the present study. Photographs sent by López Udias (pers. comm., 2020) depict a phenotype closer to *P. vulgaris* than to *P. casperiana* or *P. dertosensis*, but somehow peculiar compared to "typical" *P. vulgaris*. Such populations have to be investigated in a geographically wider study, especially comparing it to *P. vulgaris* L. var. *alpicola* Rchb., *sensu* Legendre *et al.* (2014).

A similar matter appears when it comes to the swampy populations of *Pinguicula*, in the Montes Universales, around the triple point Cuenca/Guadalajara/Teruel. The voucher MA-01-00589325 was identified as belonging to *P. mundi* in Blanca *et al.* (1999). This voucher was made from a fruiting specimen. However, the seedpod does not correspond neither to *P. casperiana* nor to *P. mundi*, but could match to the one of *P. dertosensis*. One population, at the Rio Júcar source, has been

investigated for the present study. Flowers in fact look intermediate between *P. casperiana* and *P. vulgaris*. It can be hypothesized that *P. casperiana* actually represents the saxicolous populations of the Serranía de Cuenca, while another possible new taxon occupies the swampy areas of the Montes Universales, but this point still has to be more closely investigated. In this respect, additional populations assigned to *P. vulgaris* in literature and herbarium vouchers, growing in the surroundings, would need to be investigated too.

Additional comments and discussion

As can be seen in this extract, this article was in full agreement with Crespo *et al.*'s (2020) opinion that *Pinguicula casperiana* is a distinct species from *P. dertosensis* and *P. mundii* and it gave additional diagnostic characters to discriminate them. Of course, although not explicated, "*P. conquensis*" was also considered to be different from the superficially similar *P. vallisneriifolia* and *P. saetabensis*. However, I do not consider *P. submediterranea* and *P. tejedensis* as distinct entities from *P. dertosensis*. Although it was one point I also thought to address in my article, I was not able to find any significant diagnostic character after reviewing many vouchers and pictures. The main morphological difference of *P. submediterranea* claimed by Crespo *et al.* (2020) is the smaller size of the plants in all aspects. In table 1, *Pinguicula tejedensis* and *P. submediterranea* seedpods are claimed to be oblong-ovoid, the which I cannot confirm from voucher and picture examination and from their figure 1 (see also Figure 2 in this article for comparison with *P. dertosensis*). The difference in seed shape is also not obvious (compare their figure 4 with Figure 2 in this article for comparison with *P. dertosensis*). Thus, *P. submediterranea* and P. *tejedensis* can be regarded as later synonyms of *P. dertosensis*.

The main focus of Crespo *et al.*'s study (2020) is on molecular phylogeny. *Pinguicula casperiana* is genetically closely related to *P. dertosensis*, but, as seen above, it is morphologically distinct. *Pinguicula submediterranea* and *P. tejedensis* appear genetically distant from *P. dertosensis*, although they are morphologically identical. A similar matter already occurred when describing *P. lattanziae* (De Castro *et al.* 2016). Unfortunately, Crespo *et al.* (2020) did not describe their protocol in the material and methods, but seemingly used the same as they did in Crespo *et al.* (2018), which is based on De Castro *et al.*'s (2016) material and methods. Sanger sequencing is problematic when analyzing nuclear markers of polyploid organisms. The obtained sequence is a mix of several (up to eight in the case of this group of octoploid butterwort species) sequences and thus the final result greatly depends on the interpretation of the person who analyzes the raw data. This experimenter bias will therefore also affect the subsequent molecular phylogeny analysis. Although nuclear markers will probably prove to be very useful, recent results have shown the limits of the currently applied method that is only able to discriminate groups of species, but has to be considered very cautiously at the species level. As it is, such analyses may be used to support morphological differences, but should not be the base for describing new species. A different experimental method should lead to more significant results. I designed such a protocol (unpubl.) but I hadn't yet the opportunity to apply it to butterworts. However, independent similar experiments gave interesting results on ferns (Rothfels *et al.* 2017), moonworts (Dauphin *et al.* 2018) and quillworts (Grigoryan *et al.* 2020), for example.

Acknowledgements: Eric Partrat and Laurent Legendre are thanked for useful fieldtrip pictures and accession to cultivated material. Eric Partrat is also thanked for useful discussions about *P. casperiana*. Iwein Coppens was part of the 2010 fieldtrip is thanked for driving long way down to Spain. Oliver Gluch is thanked for providing one picture to complete Fig. 4. ALBA, BC, GADC, JACA, MA and MAF curators are thanks for their kind assistance in examine their vouchers.

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An interesting example of *Pinguicula macroceras* from Vancouver Island, Canada

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Having found many populations of what is known as *Pinguicula macroceras* on Vancouver Island, we have noticed this species can vary greatly in morphology between locations. One interesting example of this is from plants found along the Gordon River on the southwest coast of the island near the town of Port Renfrew.

The habitat of the Gordon River population is notable in that it is found in seeps in proximity to karst (Fig. 1A, photo taken from cave overlooking the river). One of the seeps they are growing on originates from a spring flowing from a cliff of the river canyon at the transition between limestone and igneous rock. The other seeps in the area originate from groundwater flowing through forest soil above the canyon (Fig. 1B, typical groundwater seeps seen on the right). It is not obvious in these examples whether they have karstic influence. Given how much limestone is in the area there is a good chance they are. We have not observed any of these plants growing directly on the limestone.

What we noticed, is these plants can produce up to 6 inflorescences when fully mature (Fig. 2A) and often have 2-5. From looking into the literature, this appears to be unusual for this species. The usual number seems to be between 1-3 with a maximum of 5.

Another unusual characteristic of this population is the sometimes reduced but usually completely absent white patch on the lower corolla lobes. Often any white colouration is only present on the tips of the trichomes of the "pseudopollen lure" near the entrance of the corolla tube (Figs. 2 B & C).

Many of the *P. macroceras* from this population and the surrounding area exhibit stamen-like structures protruding from under the calyx. These structures have the angled look of insect legs (Fig. 2D) In our research, we cannot find anything describing these characteristics on other populations.

Seed collected from this location grew into plants with the same lack of a white corolla patch and propensity to be unusually floriferous (Fig. 3). None seem to be mature enough to produce more than 4 inflorescences yet, though.

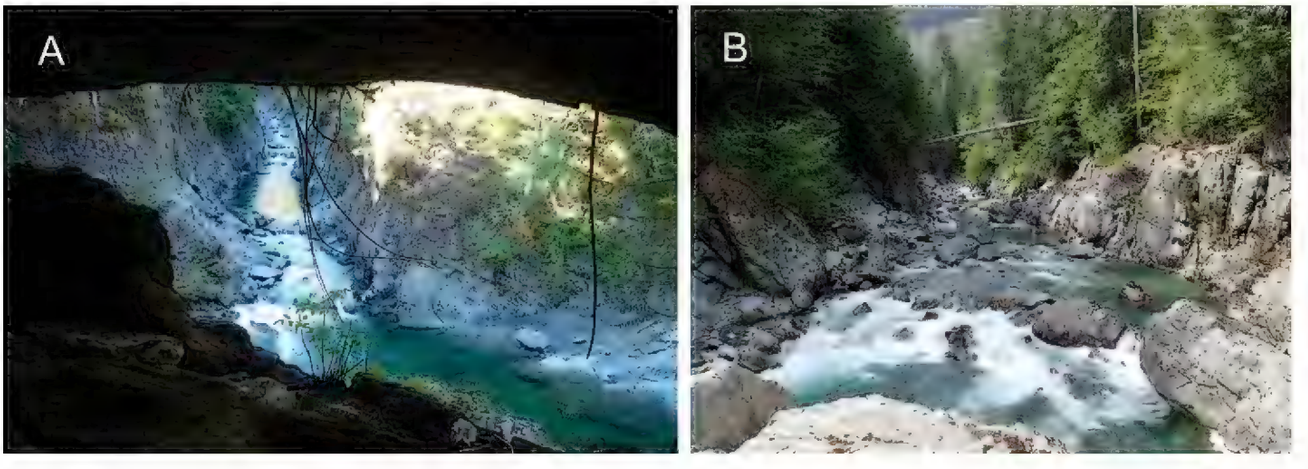

Figure 1: A) Photo taken from cave in karst overlooking the Gordon River; B) springs flowing from a cliff on the right side of the river canyon at the transition between limestone and igneous rock.

Figure 2: A) *Pinguicula macroceras* producing up to 6 inflorescences; B & C) inflorescences are usually completely absent a white patch on the lower corolla lobes; any white colouration is only present on the tips of the trichomes of the "pseudopollen lure" near the entrance of the corolla tube; D) stamen-like structures protruding from under the calyx have the angled look of insect legs.

We will continue to explore the diversity of *P. macroceras* on Vancouver Island and hope to compile our observations into a longer article. This is a look at a single population, but we have found notable examples of the diversity of this taxon at many other locations on Vancouver Island.

Figure 3: *Pinguicula macroceras* from seed collected from plants growing in seeps in proximity of karst.

Pinguicula in the Lower 48: Habitat Notes

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The "Lower 48" refers to the 48 contiguous states of the USA (i.e., excluding only Hawai'i and Alaska, but including Washington, D.C.). Within this region, there are eight species of *Pinguicula*, mostly confined to the southeastern part of the country. Since the ranges of southeastern species overlap so much, it is usually the case that the carnivorous plant botanist exploring wetland habitats is likely to encounter more than one species. Even so, the various species have subtle differences in habitat preferences.

What follows are some of my observations on general preferences. However, if you go exploring yourself, don't be surprised if plants break the rules…perhaps they haven't read my notes. And after all, one of the fun things about observing organisms in the wild, is learning how they often innovate in surprising ways!

Let's play a bizarre little thought experiment. Suppose you were descending a low hill, towards a wetland in the low country of the southeastern USA. In what order might you expect to encounter *Pinguicula* species?

Upland species

Long before you reach areas of open water, the first species you would be likely to encounter would be *Pinguicula pumila*—this species often enjoys sandy areas that are surprisingly dry. In

Figure 1: *Pinguicula pumila* in Tyler County, Texas.

some situations, the habitats may be suitable only for a portion of the year—that's ok, because the plant is perfectly happy functioning as a short-lived annual in such situations.

I find *Pinguicula pumila* truly fascinating. In parts of Florida, especially southwards towards the Keys, the plants tend to have very small, crumpled looking flowers that may be white, purplish, or yellow—in the latter case, such plants have been given the name *P. pumila* var. *buswellii*. Meanwhile, in parts of Texas I've seen much larger plants with commensurately large flowers that reminded me of *Pinguicula agnata* (Fig. 1). This variation is fascinating—are we seeing speciation at work? If humans hadn't come along, might there have been new species on the evolutionary horizon?

Dropping a few crucial centimeters in elevation, the ground becomes almost imperceptibly moister. In these locations you can start picking up *Pinguicula lutea* and *P. caerulea* (Fig. 2).

I'm talking broad strokes here. There's so much variation from site to site that the three species—*P. caerulea*, *P. lutea*, and *P. pumila*—are probably just best treated as a habitat trio.

While we are on our fictional wetland trip, make sure you take time to enjoy the variation in flowers. *Pinguicula caerulea* can vary from pure white flowers (=*P. caerulea* f. *leucantha,* Fig. 7) to lightly veined flowers, to lilac-blushed flowers, to nearly pure violet flowers. Analogously, *P. lutea* can range from white-flowered forms (*P. lutea* f. *alba,* Fig. 7), to creamy flowers, to deep yellow. The petals of *P. lutea* are particularly variable, and can range from being barely notched at the tip, to multiply divided distally into fingerlike projections (Fig. 7). Weird.

Figure 2: Left, *Pinguicula caerulea* in Onslow County, North Carolina. Right, *Pinguicula lutea* in Stone County, Mississippi.

Lowland species

If you've managed to keep your feet dry up to now, things are going to change rapidly. Dropping down a few more centimeters means we'll be in soft mucky mud, and then—dropping further—entering standing water.

Sloshing around in reedy, grassy water, especially near the edges of trees, you have a chance to encounter *Pinguicula ionantha*. (Tread carefully, as it is Federally listed as being "Threatened.") *Pinguicula ionantha* lives in this extremely delicate substrate, with its roots and lower parts in fully saturated muck (Fig. 3). Always keep an eye on flower color when enjoying *P. ionantha*—while usually creamy white, some plants can be flushed with various amounts of lilac (Fig. 7). You are likely to see little monitoring tags on the plants because their populations are closely monitored by agency botanists!

In comparably wet conditions, you're likely to encounter *Pinguicula planifolia*. This very large species often enjoys open mud flats in the bottom of seasonally filled ponds (Fig. 4). When the

Figure 3: *Pinguicula ionantha* in Liberty County, Florida

Figure 4: A crawfish seeking cover under a submerged *Pinguicula planifolia* in Liberty County, Florida.

Figure 5: A free-floating *Pinguicula primuliflora* in Walton County, Florida.

water is low, they're fully exposed on open mudflats, but during wetter times they can be in water ankle deep, or even deeper! This species is regularly pale lilac (Fig. 7), but oddly often produces flowers with abnormal numbers of petals. I've seen them with anywhere between three and nine!

Our last species to be encountered in this trip, *Pinguicula primuliflora*, also loves wet, inundated situations. However, instead of being submerged in deep water, *P. primuliflora* might be found floating on the water's surface—usually part of a vegetation mat—but occasionally floating freely on the water's surface (Fig. 5). Interestingly, *P. primuliflora* is not restricted to still water—I've seen it in riparian habitats, floating in relatively quiet, protected corners of small streams. This very charismatic species has flowers that usually have bicolored flowers—pink distally, white proximally. It is also the species most likely to bud plantlets from its leaves.

Hibernaculum-forming plants

Moving to other parts of the USA, we encounter two more species—*Pinguicula macroceras* and *P. vulgaris*. These are very similar plants—indeed they are so similar that plants in cultivation can be hard to identify confidently. In the wild, range is the easiest way to tell them apart. *Pinguicula vulgaris* is found in flat, quiet wetlands in the northeast and Great Lakes region. In terms of wetness, it prefers the same moistness as the *Pinguicula ionantha-planifolia-primulifiora* group. Meanwhile, *Pinguicula macroceras* is found in the Pacific states, and is usually found in wet seepages and cliffs (Figs. 6, 7).

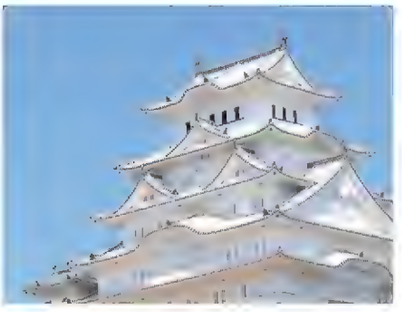
The *Pinguicula* of the Lower 48 comprise a lovely group of plants. I encourage you to seek them out and make your own habitat observations. While many of your observations will probably support my general outline above, no doubt you'll find exceptions to them as well—that is just one of the many fascinating aspects of these remarkable plants.

Figure 6: Red-tinged *Pinguicula macroceras* in Del Norte County, California.

Figure 7: Variation in *Pinguicula* flowers. Top row, left to right: *P. caerulea* f. *leucantha*, Onslow County, North Carolina; *P. lutea* f. *alba*, Liberty County, Florida; *P. lutea* with strong petal lobation, Liberty County, Florida; *P. ionantha* with white flowers, Liberty County, Florida. Bottom row, left to right: *P. ionantha* with purplish flowers, Liberty County, Florida; *P. planifolia* floral variation, Liberty County, Florida; *P. macroceras* with large white floral spot, Siskiyou County, California; *P. macroceras* with almost absent white floral spot, Wallowa County, Oregon.

13TH ICPS CONFERENCE
MAY 13–15, 2022
HIMEJI, JAPAN

The 13th ICPS Conference, which has been postponed 2 years because of the COVID-19 pandemic, will be held in Himeji City, Hyogo Prefecture from Friday, May 13 to Sunday, May 15, 2022. With the assumption that the pandemic-related travel restrictions will have been relaxed, we plan to put the original 2020 conference program into practice in May.



Himeji is renowned for Himeji Castle, a world heritage site that proudly represents the beauty of Japanese castles. The conference venue, Himeji Citizens Hall, is located a 12-minute-walk from Himeji Station and a 10-minute walk from Himeji Castle.

The 3-day conference will cover a wide range of topics, e.g., scientific researches, new discoveries and horticulture/conservation topics. Consecutive interpretation by English-Japanese interpreters will be provided for the presentations. There will be exhibitions and sales of plants in the same building from the noon of May 13 to the end of the conference.

The conference dinner is planned for May 14 at the banquet room "Ciel" on 14F of Hotel Monterey Himeji, where you can enjoy a good mix of Japanese and Western cuisines together with an impressive nighttime view of Himeji Castle.

There will be an excursion to the Tegarayama Conservatory Botanical Garden and the Hyogo Prefectural Flower Center (HPFC) on May 16. Especially in HPFC, we will be guided through the amazing collections of *Nepenthes*, *Sarracenia*, and other carnivorous plants in the CP-dedicated greenhouse as well as the backyard. You will be meeting the giant *N. clipeata* and *N. pervillei* that were introduced in the 2018 ICPS conference.

On May 17, we will enjoy a field trip to see the local habitats of *Drosera rotundifolia*, *D. tokaiensis*, and *D. lunata*. Then those who visit the *P. ramosa* habitat will travel to Tokyo for an overnight stay. On May 18, the party will have a 2-hour hillwalking to the habitat of Japan's endemic *Pinguicula ramosa* on Mt. Nyoho, Nikko City.

The Japanese Carnivorous Plant Society (JCPS) with the cooperation of the Kansai Carnivorous Plant Society (KCPS), the Tokai Carnivorous Plant Society (TCPS), and the Hiroshima Carnivorous Plant Society (HCPS) will host the 13th ICPS Conference. These 4 societies mainly cover the Kanto, Kansai, Tokai, and San-yo regions, respectively, and have been contributing to prevalence of carnivorous plants in Japan.

Although we cannot foresee when the COVID-19 is tamed globally as of mid-September 2021, we expect the situation will considerably calm down by next spring thanks to vaccination. Nevertheless, if any infection prevention measures are instructed/recommended at the time of the conference, we will faithfully apply them.

Please visit the conference web pages at the following URLs for registration.

http://jcps.life.coocan.jp/ICPS2022/ICPS2022_E.html

http://jcps.life.coocan.jp/ICPS2022/index.html <Japanese>

Looking forward to meeting/seeing you in Himeji in May 2022!

Koji Kondo - Conference Organizer Team [email: kokonchip@gmail.com]

A short profile on *Triantha* (Nutt.) Baker with a focus on *T. occidentalis* (S.Watson) R.R. Gates

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Keywords: Taxonomy: *Triantha occidentalis*.

Introduction, taxonomy, and ranges

In case you haven't heard, a recent study (Lin *et al.* 2021) has revealed that *Triantha occidentalis* is carnivorous. This is remarkable news for a number of reasons. First, *Triantha* is a monocot, and carnivory in monocots is a very rare thing indeed. Second, those few monocots that are carnivorous, are quite unimpressive in their carnivorous nature—for the most part they are only urn-forming bromeliads that passively capture prey (see the discussions of *Brocchinia* and *Catopsis* in McPherson 2007). *Triantha* is different…it is a monocot with glandular hairs, the glandular hairs release digestive enzymes, and the plant absorbs the nutrients from the captured prey into its own tissues!

What follows is a short introduction to this attractive plant, including information about this plant's closest relatives, where it grows, how to identify it in the field, some notes about its natural history and conservation status, and a little speculation about its horticulture.

There is some disagreement in how scientists organize plant relationships, and we see this here. In the Flora of North America (Packer 1993), the genus *Triantha* is classified as being in the lily family (Liliaceae). Meanwhile, in the Jepson eFlora—which is the most commonly used taxonomic authority in California—*Triantha* is placed in the false asphodel family (Tofieldiaceae; see McNeal 2012). I follow the Jepson eFlora in this respect, as did the Lin *et al.* (2021).

There are four genera in the Tofieldiaceae: *Harperocallis* McDaniel, *Pleea* Michx., *Tofieldia* Huds, and *Triantha* (Nutt.) Baker. It would be fair to say that none of these plants are particular beauties that would make the average vacationer stop their car to gawk, but after giving the plants some time to be appreciated, the astute naturalist will see that these are quite lovely.

The genus *Triantha* has four species. (*Triantha occidentalis* was formerly classified as *Tofieldia occidentalis*.) Three of them are found only in North America (the USA and Canada), while one is restricted to Japan. Their ranges are below (GBIF 2021; Packer 1993).

Triantha glutinosa (Michaux) Baker: Found in Canada and northern USA—In Canada: all the geographical regions except Nunavut; in the USA: OR, ND, MN, WI, MI, IL, IN, OH, WV, VA, NT, NC, NV, VT, NH, ME, AK.

Triantha japonica (Miq.) Baker: Only found in Japan (Chūgoku northwards to Hokkaidō).

Triantha occidentalis (S.Watson) R.R.Gates: Found in Canada and northern USA—In Canada: BC, AB; in the USA: AK, WA, ID, MT, WY, OR, CA.

Triantha racemosa (Walter) Small: Found in southeastern USA: TX, LA, MS, AL, FL, GA. Also occurs along the Mid-Atlantic coast: VA, DE, DC, MD. Populations in New Jersey may be hybrids with *T. glutinosa* (Packer 1993).

The species *Triantha occidentalis* has three subspecies: *Triantha occidentalis* subsp. *occidentalis*, *Triantha occidentalis* subsp. *brevistyla* (C.L.Hitchc.) Packer, and *Triantha occidentalis* subsp. *montana* (C.L.Hitchc.) Packer. The ranges of these three subspecies are as follows.

Triantha occidentalis subsp. *occidentalis*: USA (OR, CA)

Triantha occidentalis subsp. *brevistyla*: Canada (BC, AB), USA (AK, ID, WA, OR)

Triantha occidentalis subsp. *montana*: Canada (BC, AB), USA (AK, ID, MT, WY)

In California, the plant is found mostly in three large range segments. The first range segment is the northwest portion of the state (especially the Klamath Ranges). The second and third range segments are in the Sierra Nevada, ranging from Lassen Volcanic National Park southwards to (and somewhat past) Sequoia and Kings Canyon National Parks. This long range is divided into two segments by an apparent absence of occurrences in Alpine, Amador, and Calaveras Counties. Other reports exist for this plant in Sonoma County and Marin County, although the ones from Sonoma County are quite old (1928-1972) and in regions that have experienced significant habitat modification.

The authors in Lin *et al.* (2021) treated *Triantha occidentalis* at the species level, and did not comment on possible differences in carnivory at a subspecific level. Their field work used specimens of *Triantha occidentalis* subsp. *brevistyla* (Lin, pers. comm. 2021) from Cypress Provincial Park, British Columbia, Canada. In their illustrations they included supporting imagery of *Triantha occidentalis* subsp. *brevistyla* from North Cascades National Park in Washington (USA), but also *Triantha occidentalis* subsp. *occidentalis* from California (USA). The inference would be that the authors consider carnivory to be the case throughout the species.

Identifications

There are many monocots with basal rosettes of long leaves, and which have white flowers on racemes, so I will not give here comprehensive guidelines to identify which of these are *Triantha*. But in my region (California), if you find such a plant, and you further observe that it has superior ovaries and three styles, six more or less similar tepals that are not fused to each other, and filaments that are glabrous, it is very likely you are looking at *Triantha*. Confirm the identification in your local flora!

Some additional hints follow. Consider range…that might make your identification easy. Cultivated plants (or those in range overlap zones) present more challenges, and in such cases you will need plants in flower (and perhaps fruit).

First, let us identify the three plants in the genus to species. *Triantha racemosa* is easiest to distinguish from the others—its three styles are fused from their bases upwards for 1/4 to 2/3 their length, while the styles of *T. occidentalis* and *T. glutinosa* are distinct.

It is more difficult to tell *T. occidentalis* from *T. glutinosa*. The easiest metric is to look for a white seed coat that encloses the dark reddish seed—this coat is present on *T. occidentalis*, but absent on *T. glutinosa*. Lacking seeds, look for long glandular hairs just below the inflorescence, or a globose shape to the inflorescence: *Triantha glutinosa* lacks long glandular hairs or globose flower heads, while (depending on the subspecies) these characters may be expressed in *T. occidentalis*.

If you are confident that you have *Triantha occidentalis*, you should try to identify it to subspecies. Our current understanding of the subspecies indicates overlapping ranges for subsp. *brevistyla* with subsp. *montana*, and subsp. *brevistyla* with subsp. *occidentalis*. Reproducing (stealing!) the key from Flora of North America (http://floranorthamerica.org/Triantha_occidentalis) indicates a number of useful features:

1a. Seed coat not strongly inflated; seeds 3-4 times longer than wide; stems coarsely glandular-pubescent with cylindrical hairs below inflorescence, hairs 4-6 times longer than wide, or glands absent → *Triantha occidentalis* subsp. *montana*

1b. Seed coat strongly inflated; seeds usually 1-2(-3) times longer than wide; stems glandular-pubescent below inflorescence, with glands ½-2 times longer than wide, or pubescent with cylindrical hairs 2-4 times longer than wide, sometimes glands and hairs intermixed → 2

2a. Styles 0.6-1.5 mm; inflorescences usually cylindrical-ovoid → *Triantha occidentalis* subsp. *brevistyla*
2b. Styles 1.3-3 mm; inflorescences usually globose → *Triantha occidentalis* subsp. *occidentalis*

With some practice and appropriate materials, these key features should be reliably diagnostic. The only complications that have been found is that *T. occidentalis* subsp. *occidentalis* and *T. occidentalis* subsp. *brevistyla* might intergrade in southwest Oregon (Packer 1993). Furthermore, *T. occidentalis* subsp. *occidentalis* in Del Norte County (California) and Josephine County (Oregon) might be atypically large, with elongate inflorescences (Packer 1993; pers. obs.).

Natural history and conservation

Triantha occidentalis produces a rosette of linear, basal leaves up to 50 cm tall and nearly 1 cm wide. Each inflorescence is a single, naked scape up to 80 cm tall (Fig. 1A). It reportedly can bear a

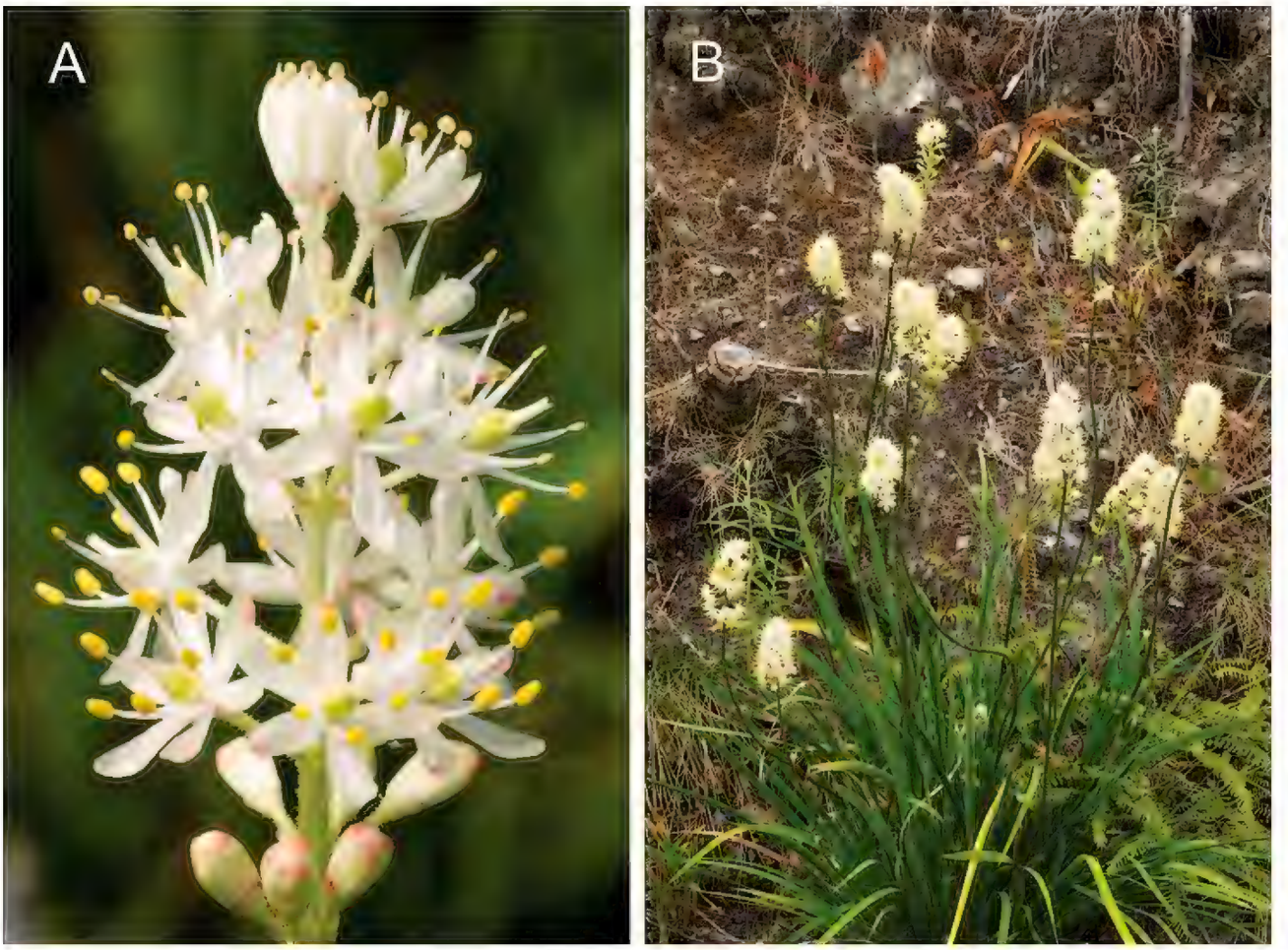

Figure 1: (A): *Triantha occidentalis* subsp. *occidentalis* in Plumas County (California). Can you see the small, glandular hairs on the inflorescence, and also can you see the groupings of flowers in threes? (B): *Triantha occidentalis* subsp. *occidentalis* in Del Norte County (California). The inflorescences of these plants are so large, they start to look like *Toxicoscordion* (=*Zigadenus*), in the closely related family Melanthiaceae.

few leaves on it, but I have not yet observed this. Each plant can produce a number of inflorescences. The flowers are clustered near the top of the inflorescence in a fairly dense cluster. This cluster is usually globose, but elongated clusters are to be expected, especially near the Oregon-California border (Fig. 1B). The flowers tend to be produced in little clusters of three flowers, which is the origin of the name *Triantha*.

The flowers have six blunt tipped tepals (the three sepals and three petals are, to my eye, nearly identical) 3-7 mm long. The filaments are white, stout, and nearly as long as the tepals. The anthers are bright yellow. The elongate superior ovary is topped by three distinct styles. The inflorescence bears short, stalked glands, which is of course why you are reading about the plant in this journal. Fruit are capsules that bear reddish brown seeds about 1 mm long, encased in a white coat. The fruit can become tinged with red, and are sometimes more eye-catching than the flowers!

I have never had any reason to dig around a plant, but it reportedly has short spreading rhizomes, and as such probably can reproduce vegetatively by natural division.

I have seen it growing in full sun and partial shade. In California I have found it in wet seepages, wet meadows, floating sphagnum bogs, or riparian areas (Fig. 2). I have found growing at carnivorous plant sites that contain *Darlingtonia californica*, *Drosera anglica*, *Drosera rotundifolia*, *Drosera* × *obovata, Pinguicula macroceras*, *Utricularia macrorhiza*, *Utricularia intermedia*, *Utricularia ochroleuca*, and *Utricularia minor*), but it is certainly not picky. It is even reported in non-wetlands (Calflora 2021).

In California, it flowers over a long season (depending upon altitude and exposure of the site), typically from July through September (Calflora 2021).

Figure 2: Can you see it? In the photo center, there is a single rounded head of *Triantha occidentalis* subsp. *occidentalis* in this Siskiyou County (California) *Darlingtonia* and *Drosera rotundifolia* lakeside habitat. There's also *Utricularia macrorhiza* and *Utricularia minor* present, but not visible in the photo.

In terms of conservation status, *Triantha* does not appear on any rarity lists, either state or globally. It has a wide range, and occurs in many sites in the wild. That said, I expect the extraordinary fire seasons we are now experiencing in the western USA, exacerbated by global climate change, will significantly impact many wetland sites. Even if the sites do not themselves burn, they may be subject to harmful impacts because of post-fire sedimentation and overall changes in hydrology.

As yet, poaching is not an issue. Unfortunately, I know the culture of carnivorous plant horticulturists, and the presence of bad apples, and fully expect to start hearing about plants being dug from the wild. I would strongly discourage against such practices. If collection is to be done, collect seeds within the framework of state and local laws, please.

Guesses on cultivation

This is not a particularly showy plant, and is unlikely to be encountered for sale except by native plant specialty nurseries. Looking online, I have only found one source for seeds, which recommends a cold, wet stratification period of 60-90 days (Klamath-Siskiyou Native Seeds 2021).

I suspect that this plant is not particularly challenging to grow, if you followed a general cultivation method appropriate for carnivorous plants such as *Sarracenia* or *Darlingtonia*. I would try a low nutrient, neutral to acidic pH medium. Remember that it grows outside in an area with significant winter snowfall, so give it a good cold rest.

It is likely that this plant will divide naturally via rhizome multiplication. I have seen multiple-headed plants in the wild, and suspect that they resulted from natural division.

This is all new terrain, and it will be interesting to see the results, as carnivorous plant growers turn their attention towards cultivating this plant. Does it require cross pollination? Is stratification really necessary? Will it respond well to fertilization? Will it turn out to be an inexplicably difficult plant to grow? Time will tell. But please…do make sure you obtain your plant propagules responsibly. I challenge growers not to field collect plants!

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Obituary: Allen Lowrie 1948 – 2021

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It was with great sadness we learnt Allen Lowrie passed away in August of this year. Allen was a world authority on Carnivorous Plants and Triggerplants, and an active contributor to our community to the end.

Allen authored 6 books on Australian Carnivorous Plants and co-authored 3 further works on the *Drosera* of the world and has written many scientific papers naming the many new species of plants he discovered. During his botanical career Allen named 135 new plant species and his name is honoured in two carnivorous plant species, *Drosera lowriei* and *Utricularia lowriei* and the triggerplant *Stylidium lowrieanum*. An accomplished artist, Allen also produced all of the botanical drawings and illustrations for his books and papers. Beyond his botanical pursuits, Allen was a keen musician, playing guitar, rhythm, lead and bass, the mandolin, and keyboards and recorded no fewer than 30 songs. Aside from his many botanical achievements, Allen spent countless hours corresponding with CP enthusiasts and scientists across the globe and was always happy to share his vast knowledge, especially to eager young beginners. Many a plant collection the world over has material of Pygmy, Tuberous and Tropical *Drosera* brought into cultivation through Allen's work with these plants. Allen was a unique character and will be greatly missed. We pass on our sincere condolences to his wife, Pauline, daughters, Trinity and Filicity, and grandchildren, Evan, Yana, and Lochlan.

The March 2022 CPN will be dedicated to Allen and will also feature a comprehensive update on the Carnivorous Plants of Australia, to be read alongside Allen's benchmark 2014 work, *Carnivorous Plants of Australia Magnum Opus*.

Allen Lowrie with *Nepenthes rowaniae*, Cape York, Australia, 2008. Photo by Richard Nunn.

New cultivars

Keywords: cultivar, *Cephalotus* 'Tom Thumb', *Dionaea* 'Carboni Ardenti', *Dionaea* 'F.S. Colombian Dwarf Caiman', *Dionaea* 'F.S. Anemone', *Dionaea* 'Periscope', *Nepenthes* 'Candy Apple', *Sarracenia* 'Joker', *Sarracenia* 'White Beast'.

Abstract: Eight new carnivorous plant cultivars are named and described: *Cephalotus* 'Tom Thumb', *Dionaea* 'Carboni Ardenti', *Dionaea* 'F.S. Colombian Dwarf Caiman', *Dionaea* 'F.S. Anemone', *Dionaea* 'Periscope', *Nepenthes* 'Candy Apple', *Sarracenia* 'Joker', *Sarracenia* 'White Beast'.

Dionaea 'Carboni Ardenti'

Submitted: 16 July 2021

Dionaea 'Carboni Ardenti' (Fig. 1) was selected in 2019 by Valerio Guidolin from Diflora. This cultivar came from an in vitro random mutation of Diflora's *Dionaea* 'Periscope' which derives from *Dionaea* 'Microdent' × 'Cupped Trap'.

Similar to *Dionaea* 'Microdent' it has different colors especially the inner trap's side, a larger number of trigger hairs, and also different cilia.

The unique phenotype of *Dionaea* 'Carboni Ardenti' shows short cilia and a high number of trigger hairs in the inner orange-red coloured traps side. The name "carboni ardenti" means burning coals and was choosen by Valerio Guidolin because he imagined that the inside trap is similar to "walking on burning coals" for an insect.

Dionaea 'Carboni Ardenti' is a unique cultivar that can only be propagated by leaf/floral or rhizome cuttings to preserve the phenotype.

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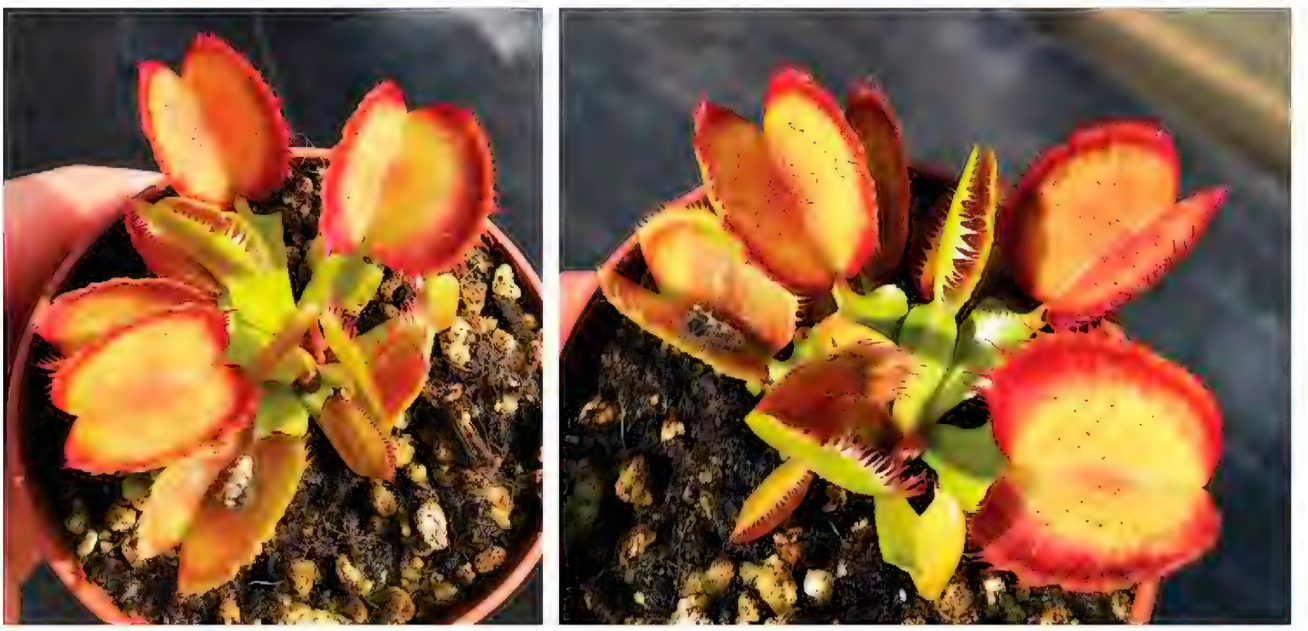

Figure 1: *Dionaea* 'Carboni Ardenti'.

Submitted: 15 July 2021

Dionaea 'Periscope' (Fig. 2) was produced in 2016 by Paolo Mattevi by breeding *Dionaea* 'Microdent' with *Dionaea* 'Cupped Trap'. Numerous seeds from this breeding were germinated in vitro by Valerio Guidolin of Diflora. From subsequent growth of these seedlings, *Dionaea* 'Periscope' was selected as a unique phenotype.

Dionaea 'Periscope' is characterized by small green leaves with large deep red traps that show the unique red outline, traps are also wide with *D.* 'Microdent' like short cilia, but more dense and big trigger hairs that are fully functional.

The name "periscope" was chosen in July 2021 by Valerio Guidolin because of the rotated traps that sometimes *Dionaea* 'Periscope' shows.

Dionaea 'Periscope' must only be propagated by leaf/floral or rhizome cutting to preserve the phenotype.

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Figure 2: *Dionaea muscipula* 'Periscope'.

Dionaea 'F.S. Colombian Dwarf Caiman'

Submitted: 10 June 2021

While cultivating typical *Dionaea muscipula* from the FloraSalvaje Lot (F.S.) of the Engineer Juan Camilo Páez Jiménez, a unique specimen was noted and separated for further growth and study. These unique characteristics persisted and the plant is given the cultivar name *Dionaea* 'F.S. Colombian Dwarf Caiman'.

The plant has pale yellowish green tones which maintains the same coloration under full sunlight (Fig. 3A). The leaves are wide and about 3-4 cm long with a slight inward curvature with no noticeable midrib. There is a short petiole between the leaf and the trap. When the trap is forming there are no teeth, just jaws or gums (Fig. 3B). The traps are elongated and have an inward curvature of the lobe as if it formed gums. As it grows its lobes thicken and internally the lobe produces a soft orange coloration. The trap eventually develops teeth and fangs that go inward like the dwarf caiman with a pronounced jaw or gum (Fig. 3B). Over time, in some cases, some of the teeth come out of the closed trap (Fig. 3B, C). The teeth are 5 mm long. There are 4 trigger hairs with almost transparent coloring.

Dionaea 'F.S. Colombian Dwarf Caiman' has a perfect thick gum, uniform and sharp teeth that enter the trap almost touching the trigger hairs, disarticulated lobes, imperceptible transparent trigger hairs, growth of longer and wider leaves, internal green coloration in the trap when in direct sun, the trap does not have a long curvature and has a high reproductive capacity through dividing. These are some marked differences compared to cultivars like *D.* 'Alien' and *D.* 'Louchapates'. *Dionaea* 'Jaws Smiley' is slow growing, the lobes are attached laterally, and the interior is crimson-red in direct sunlight, the traps are long and slightly curved, the trigger hairs can be noticed, the petioles are short (making them stiff or narrow), it has teeth between short and long interspersed that do not enter the lobe when they are closed, they do not leave teeth outside the trap; these are contrary characteristics when compared to *D.* 'F.S. Colombian Dwarf Caiman'.

The name 'Dwarf Caiman' lies in the resemblance of its cilia with the teeth and fangs of a dwarf caiman located in the Orinoquia or Amazon of our Colombian area. Another reason for selecting this name is to enhance the Colombian wildlife. 'Colombian' is because we are proud that it is the first cultivar of *Dionaea* from Colombia.

—Juan Camilo Páez Jiménez • and • Maribel Bohórquez Rodríguez • FloraSalvaje • BioEspacio SAS • Bogotá D.C. • Colombia • florasalvajeteatrapa@gmail.com

Figure 3: *Dionaea* 'F.S. Colombian Dwarf Caiman'. A) Plant; B) trap forming, no teeth (bottom) and a few teeth emerging (left); C) mature trap with some teeth outside the trap.

Dionaea ‘F.S. Anemone’

Submitted: 28 July 2021

While cultivating seedlings from cross-pollinated typical *Dionaea muscipula* from FloraSalvaje (F.S.) of the Engineer Juan Camilo Páez Jiménez, a unique specimen was noted and separated for further growth and study. After two years, its particular dental characteristic persisted and the plant is given the cultivar name *Dionaea* ‘F.S. Anemone’.

The plant is lemon green with a slight yellow coloration (Fig. 4). The leaves grow in the shape of a rosette and can reach an average size of 2.5 cm wide and 5 cm long. The petiole has a remarkable width with a heart shape and wrinkles in the upper curves, in addition to its young leaves being wavy. There is no midrib or it is very small in size, facilitating a close connection between the leaf and the trap. The traps are rigid with medium opening capacity. In direct sunlight, the exterior of the lobe produces a faint orange coloration. The average size of the traps is 1.5 cm wide × 2 cm long. It is an active cultivar, but when closing its traps, they tend to hit their teeth and become scattered. The main characteristic is its tentacle-shaped cilia that are directed towards different positions, giving the impression that they are sensitive. Their spiny cilia can bend both outward and sideways. There are 6 trigger hairs with transparent coloring.

Dionaea ‘F.S. Anemone’ has a similar shape with several *Dionaea* cultivars, but the growth of its teeth in a dispersed and independent way makes us differentiate it from cultivars such as *D.* ‘Cross Teeth’ and *D.* ‘Fused Tooth’ where the teeth intersect and fuse. *Dionaea* ‘Phalanx’ and *D.* ‘Paradisia’ produces its long, straight teeth, unlike *D.* ‘Anemone’ that produces short, bent teeth. Its thin, spiny teeth differ from the serrated teeth of cultivars such as *D.* ‘Sawtooth’, *D.* ‘Bristle Tooth’, and *D.* ‘FTS Lunatic Fringe’.

The name was selected because the anemone has long, flexible, and mobile tentacles that bear a great resemblance to the teeth of the traps of this cultivar. In addition to resembling the wild spirit and the hunting mode of the sea anemone.

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Figure 4: *Dionaea* ‘F.S. Anemone’.

Nepenthes ‘Candy Apple’

Submitted: 29 August 2021

Nepenthes ‘Candy Apple’ (Fig. 5) is a curious specimen from the complex hybrid *Nepenthes* ((‘Rokko’ × *boschiana*) × *veitchii*) × *veitchii* which was produced by Geoff and Andrea Mansell of Exotica Plants, Australia. This plant was grown in my collection since May of 2020 and was selected and named after it started producing mature pitchers in January 2021. Since I first obtained the plant, I had noticed that it maintained a widely flared peristome even when aged. However, I only made this selection after the plant matured when the pitchers then became extremely waxy on the exterior and gained an intense red coloration, which distinguished this specimen from the other plants I have seen of this same hybrid grex.

The name ‘Candy Apple’ was chosen because in both waxiness and coloration, the pitchers of this plant are reminiscent of the candy dipped apples commonly seen at the seasonal fairs in my home state of Massachusetts. Notably, the pitchers of this cultivar open with a very bright yellow and striped peristome which very gradually darkens to a honey color, it also has a very dense, but short, indumentum all over the pitchers, leaves, and stems.

This plant grows well in intermediate conditions; however, the best coloration is seen when the plant is given cooler nights along with very bright light.

To maintain the unique characteristics of this plant, it should only be propagated by stem or basal cuttings, the latter of which it produces prolifically.

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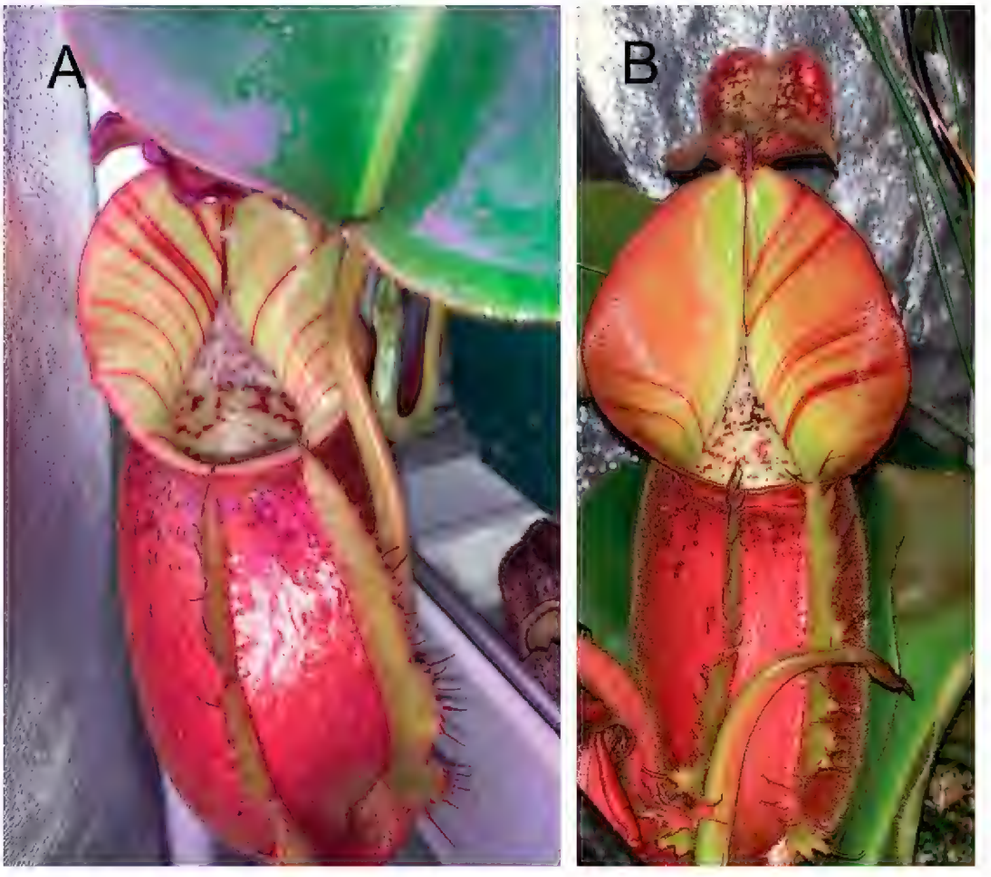

Figure 5: *Nepenthes* ‘Candy Apple’. A) Freshly opened pitcher displaying peristome and body coloration. B) Aged pitcher displaying the flared peristome characteristic, along with its short but dense indumentum.

Sarracenia 'Joker'

Submitted: 29 October 2020

Sarracenia 'Joker' was grown from seed in 2012 whose parents are ((*Sarracenia leucophylla* × *flava* var. *rugelii*) × *moorei* 'Leah Wilkinson') × *moorei* 'Adrian Slack'.

Sarracenia 'Joker' is a tall upright clone. The tallest recorded pitcher is 80 cm. The peristome is 9 cm wide. The lid is wider than the peristome and dips forwards. From above, the lid is predominantly white with a few veins. Inside the lid is white with red veins and the throat of the pitcher is a solid red blotch from one end to the other (Fig. 6).

Named in 2019 after the character 'The Joker' from the Batman films. The solid red throat resembles the eccentric makeup used to emphasise the insanity of the character and the dipping wavy lid resembles the crazy hairstyle of the character.

The cultivar needs to be propagated by vegetive means to keep the unique character of the clone.

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Figure 6: *Sarracenia* 'Joker' pitcher (left) and lid (right).

Cephalotus follicularis 'Tom Thumb'

Submitted: 3 September 2021

I wish to dedicate this cultivar to Dimitar (Dimi) Daskalov, a very dear friend of mine who recently passed away. We met via CPUK Forum many years ago through a common love for *Cephalotus* and stayed strong friends. Dimi was an avid Bulgarian *Cephalotus* grower who at one time had a very large collection of named clones and cultivars.

Dimi received this clone in Europe from a U.S. grower in 2014 and passed a division on to me in 2015. The original source is not known, nor is it known if it was more widely distributed in the USA.

Dimi was a very generous grower, and he would often send me clones without asking for anything in return. Like myself, he eventually reduced his collection to those clones for which he considered to have truly unique forms, with two of his favourites being *Cephalotus* 'Bananito' and *Cephalotus* 'Squat', the latter of which he registered as a cultivar.

Dimi and I collaborated in naming *Cephalotus* 'Tom Thumb' and authoring this description. The description was published online, but until now has never been submitted for cultivar name registration. I have been growing this clone ever since receiving it from Dimi in 2015 and it still maintains its diminutive pitcher size.

Cephalotus 'Tom Thumb' (Fig. 7) has an easily distinguishable characteristic in that the pitchers are miniature, typically measuring no greater than 1.5 cm from the base to the top of the peristome. As typical of *Cephalotus*, pitcher size for a particular clone is a function of environmental conditions, but given identical conditions, thus far this clone has shown to create smaller pitchers than typical. The shape of the base of the pitcher is hooked and acutely tapered.

Under certain conditions, the pitcher colour is very dark maroon, with the base of the pitcher taking on the deepest colouration, graduating up the pitcher. However, colouration does not form part of this clones' distinctive characteristics, as typical of *Cephalotus*, colour can vary greatly under different growing conditions, rather it is the small pitcher size that makes this clone distinctive and worthy of recognition.

Etymology: Tom Thumb is an English folklore character of diminutive stature.

Asexual propagation (vegetative) is required to preserve the clones' unique characteristics.

Dimi's soul will live on in my memories and I hope this clone and the others he loved and advocated will serve as a record in history of a fantastic *Cephalotus* grower. RIP my friend Dimi.

—Carl Leach • Aberdeenshire • Scotland • and • Dimitar Daskalov • Plovdiv • Bulgaria • carlleach@gmail.com

Figure 7: *Cephalotus follicularis* 'Tom Thumb'. A) plant, B) mature pitcher 1.4 cm, C) typical *Cephalotus* pitcher (left) and *Cephalotus* 'Tom Thumb' pitcher (right). Photos by Dimitar Daskalov.

Sarracenia leucophylla 'White Beast'

Submitted: 4 September 2021

Sarracenia leucophylla 'White Beast' is a *S. leucophylla* crossing made in 2016. This particular seedling really stood out because of its vigorous growth and nice white colour. As the seedling grew larger, the very big mouth got my attention.

The adult plant stands out because of this feature (Fig. 8). In the spring it produces a set of phyllodia and pitchers which already stand out in size compared to other *S. leucophylla* plants. The big and nice purple/red flowers are in size comparable with that of a *S. flava* flower. In late summer and autumn, it produces many full-sized pitchers. The sturdy and yet elegant pitchers are about 80 cm in height (grown in west Germany) but I expect they can grow even larger when cultivated in a warmer climate. The mouth of the pitcher has a very wide somewhat angular opening and a width of 8.5 cm is no exception. The opening stays very wide all the way down to the bottom of the pitcher. The lid is usually about half a centimeter less wide than the mouth, which makes it rather small in comparison. The colour of the pitcher is a very nice white and the veining varies from green till brown-reddish depending on the time of the year.

The name 'white beast' was given because of its big and beasty appearance in comparison to other *S. leucophylla* plants.

—Mark Geurts • Plante Carnivore Mark • Germany • rhizoompjes@outlook.com

Figure 8: *Sarracenia leucophylla* 'White Beast' plant, pitcher, and flower.